ORIGIN OF TUNDRA BUTTERFLIES IN ALBERTA

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ABSTRACT

Four distribution types are recognized in the tundra butterfly fauna of Alberta. These indicate two source areas. The major source area was south of Wisconsin ice in northern Washington, Idaho, and Montana. Nine taxa survived in this unglaciated area, five with a Southern Montane distribution: Lycaena phlaeas arethusa *(Wolley-Dod 1907),* Lycaena snowi snowi *(Edwards, 1881),* Oeneis polixenes brucei *(Edwards, 1891),* Oeneis bore edwardsi *dos Passos, 1949, and* Oeneis melissa beani *Elwes, 1893. The remaining four have a Central Montane distribution:* Colias nastes streckeri *Grim-Grschimaillo, 1895,* Boloria astarte *(Doubleday, 1846-1852(1847)),* Boloria alberta *(Edwards,Edwards 1890)* Euphydryas editha beani *Skinner, 1897. This refugium was restricted on the north by the presence of ice, and on the other three sides by lack of suitable habitat, indicating a narrow and discontinuous tundra belt south of Wisconsin ice. With retreat of Wisconsin ice, dispersal north was stopped by the elimination of continuous tundra in mountain valleys.*

Taxa with disjunct populations or endemic forms survived glaciations in an Albertan refugium in the vicinity of Mountain Park. The Albertan refugium did not contribute significantly to the colonization of present day Alberta tundra. Disjunct distribution is shown by Boloria improba youngi *(Holland, 1900). Endemic forms are* Boloria eunomia nichollae *(Barnes and Benjamin, 1926),* Boloria napaea reiffi *Reuss, 1925, and an ecological form of* Oeneis melissa beani *Elwes, 1893.*

This investigation yielded information on two isolated refugia. Therefore, the study of butterfly distribution patterns is deemed of great potential value in the study of Wisconsin glacial refugia in general.

On reconnaît quatre types de distribution parmi la faune albertaine des papillons diurnes de la toundra. Ces types indiquent qu'il existe deux régions d'origine pour ces papillons. La principale est située sud de la calotte glaciaire du Wisconsin dans le nord des états de Washington, de l'Idaho et du Montana. Dans cette région, qui échappa à la glaciation, neuf taxons ont survécu, dont cinq sont distribués dans l'étage montagnard sud; ce sont: Lycaena phlaeas arethusa *(Wolley-Dod, 1907),* Lycaena snowi snowi *(Edwards, 1881),* Oeneis polixenes brucei *(Edwards, 1891),* Oeneis bore edwardsi *dos Passos, 1949, et* Oeneis melissa beani *Elwes, 1893. Les quatre autres taxons occupent l'étage montagnard central; ce sont:* Colias nastes streckeri *Grum-Grschimaillo, 1895,* Boloria astarte *(Doubleday 1846-1852 (1847)),* Boloria alberta *(Edwards, 1890) et* Euphydryas editha beani *Skinner, 1897. Cette zone refuge était limitée au nord par la calotte glaciaire, et sur ses trois autres côtés, par l'absence d'habitats propices, indiquant que la ceinture de toundra était étroite et discontinue au sud de la calotte glaciaire du Wisconsin. Avec le retrait de la calotte, la dispersion vers le nord fut interrompue par l'élimination des zones continues de toundra dans les vallées de montagne.*

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Des taxons à populations disjointes ou des formes endémiques ont survécu aux glaciations dans un refuge albertain situé près de Mountain Park. Ce refuge ne contribua pas de facon significative à la colonisation de la toundra albertaine actuelle. Une distribution disjointe apparaît chez Boloria improba youngi *(Holland, 1900). Les formes endémiques sont représentées par* Boloria eunomia nichollae *(Barnes et Benjamin, 1926),* Boloria napaea reiffi *Reuss, 1925, et par une variété écologique d'*Oeneis melissa beani *Elwes, 1893.*

Cette recherche fournit de l'information sur deux refuges isolés. Par conséquent, l'etude des patrons de distribution des papillons est considérée comme ayant une grande valeur potentielle dans l'étude des refuges de la période glaciaire Wisconsin.

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INTRODUCTION

Certain butterfly taxa have long been recognized as having relict distributions which reflect Pleistocene events (Grote, 1875; Maynard, 1886; Holland, 1898). In spite of the early recognition of these relict taxa, few subsequent workers have considered butterflies in studies of suspected refugia in North America.

Yet butterflies would seem to be subjects well suited to such studies for two reasons. In terms of numbers of species, butterflies form an important part of the tundra community. There are more species of butterflies on the arctic islands than there are of the order Coleoptera (Ryan, 1977). This indicates a high probability that they might survive the conditions of a tundra refugium. A second reason is that butterflies appear to differentiate more rapidly than many other insect taxa (Ford, 1946). This suggests that butterfly taxa surviving in a small refugium might develop endemic tendencies to a greater extent than other insects.

A number of tundra refugia of this type have been suggested in North America, but few have escaped criticism. One that has, is in the area of Mountain Park, Alberta, Canada (see figure 1). This area is easily accessable and so became the focal area of this study.

The objectives of this paper were to determine the value of the distributions of Alberta s tundra butterflies to the study of Wisconsin age refugia. This entails the location of source areas, routes of immigration, and barriers to dispersal. In order to meet this objective, detailed distribution maps of all North American were compiled.

MATERIALS AND METHODS

Materials

During the course of this study, 1124 specimens were collected in Alberta and British Columbia, of which 907 represent taxa known to occur in Alberta. A further 720 specimens were examined from private collections, making a total of 1844 specimens.

Specimens collected within the boundaries of Banff and Jasper National Parks are deposited in the Canadian National Collection, Ottawa, Ontario; University of Alberta Strickland Museum, Edmonton, Alberta; and Park offices in Banff and Jasper. Remaining specimens are deposited as follows: voucher specimens to the University of Alberta Strickland Museum, and selected series to my collection. Some material was exchanged for specimens for future research.

Methods

A tundra butterfly species is a taxon in which the life cycle is confined to areas above treeline. This definition includes both arctic and alpine taxa. The existence of tundra is usually defined through reference to treeline. Treeline is here used to delineate the lower, or southern, boundary of the subarctic or subalpine zone as defined by Löve (1970). This is necessitated by the occurence of tundra butterfly taxa south of the actual limit of trees.

Because of limited dispersal abilities of most species used as ndicators of refugia, and the island nature of alpine tundra, taxa restricted to tundra provide the best biological evidence for identifying sites of suspected alpine refugia.

Because this study is not a revision, subspecies were accepted as presented in dos Passos (1964), as modified by more recently published information. None of these subspecies has been adequately investigated. Although many may not be valid taxonomically, the names provide convenient sources of reference to recognizably distinct populations. This is the sole reason for their use in this study. Most subspecies of in Alberta are fairly distinct, and are readily placed with populations outside the province. This allows reasonably secure hypotheses about their evolution and dispersal into Alberta.

Study area

The area under study includes all known tundra examined for butterflies in North America, but the focus of attention is on tundra in Alberta. Tundra extends from the Sierra Nevada of California and the Sangre de Cristo range of New Mexico (approximately 36° N.) at elevations of over 3384 meters (11,000 ft.), north to the limit of land on Ellesmere Island and Greenland (approximately 83° N.). In eastern North America, isolated areas of tundra occur as far south as Mount Marcy, New York, and Mount Washington, New Hampshire (approximately 44° N.) at elevations of just over 1358 meters (5000 ft.).

In Alberta, tundra extends from the United States border (49° N.) north to about 56° 20 N., where the Rocky Mountains are extended west of the provincial boundary. province. Occurrence of tundra roughly parallels the Alberta-British Columbia border along the continental divide. It is usually above 1970 meters (6500 ft.) in northern areas of the province, gradually increasing in elevation to the point where it is not found below 2153 meters (7000 ft.) at 49° N.

Results

The following tundra butterfly taxa have been reported from North America.

Where possible, sequence and classification follow dos Passos (1964). Numbers preceding names refer to this ordering. Changes reflect recent descriptions or instances where status of taxa have been questioned. Asterisks preceding a name indicates that the taxon has been recorded from Alberta.

243 *Parnassiius eversmanni thor* H. Edwards, 1881
Type-locality; upper reaches of the Yukon River.

Geographical Distribution. – Known distribution is given in Figure 2. This species is also recorded from arctic Europe and Asia, southward on numerous mountain ranges, with one disjunct population in Japan. In North America, this subspecies has dispersed outside of Beringia only to adjacent mountain ranges in British Columbia, where it is represented by two populations whose ranges are disjunct from one another.

Material examined: 88 specimens.

285 *Colias boothii* Curtis, 1835
Type-locality: Boothia peninsula, North West Territories.

Notes. –

Adults of this species have been confused by taxonomists in the past with those of *C. nastes* and *C. hecla,* and the species was once thought to represent a hybrid of these taxa. It is now recognized as a distinct species, but some taxonomists still confuse specimens with those of yellow populations of *C. nastes* , particularly *C. n. thula* (Philip, in The Lepidopterists' Society season Summaries, 1974, 1975, 1976). Populations of *C. n. thula* are sympatric with those of *C. n. aliaska*. This indicates three possibilities: *C. n. thula* is a spcies distinct from both *C. boothii* and *C. nastes; C. n. thula* is an Alaskan subspecies of *C. boothii*; *C. n. thula* is a form of *C. nastes* not deserving taxonomic recognition. Because neither *C. n. thula* or *C. boothii* are found in Alberta, this problem does not affect the outcome of this project.

Geographical Distribution. –

Distribution is indicated in Figure 3, along with that of *C. n. thula* which is plotted here to show that the two are allopatric. *C. n. thula* is restricted to northern Alaska, *C. boothii* to the North West Territories and the Yukon Territory.

Material examined: 2 specimens.

296 *Colias nastes* Boisduval, 1832
Seven subspecies are currently recognized.
C. n. nastes Boisduval, 1932
Type-locality: Labrador (Ungava Peninsula).
C. n. rossi Guenee, 1864
Type-locality: Boothia Peninsula, North West Territories.
C. n. moina Strecker, 1880
Type-locality: Churchill, Manitoba.
* *C. n. streckeri* Grum-Grschimailo, 1895
Type-locality: Laggan, Alberta (Lake Louise).
C. n. cocandicides Verity, 1911
Type-locality: unavailable.

C. n. thula Hovanitz,
Type-locality: Meade River, Alaska.
C. n. aliaska Bang-Haas, 1927
Type-locality: unavailable

Notes. –

C. n. streckeri includes only green colormorphs, which exhibit slight, but constant variation. Adults were first collected on a number of mountains in the vicinity of Laggan, Alberta, by T. E. Bean. It has since been reported from many mountains in Alberta. Colonies probably exist in the province wherever tundra has developed. Specimens are usually abundant, although often difficult to catch. Populations from Pink Mountain, British Columbia, are provisionally assigned to this subspecies.

This species has not been adequately treated in a revision. If it were, it is probable that some of the presently accepted names would be synonymized.

Geographical Distribution. –

Distribution is shown in Figures 3 and 4. This species is also known from Europe and Asia. In North America, it is recorded from Alaska, Yukon and North West Territories, Quebec, Manitoba, Labrador, British Columbia, Alberta, Washington, and Montana. Alberta distribution is indicated in Figure 24.

Exact limits of the subspecies are not known in the arctic, although the range shown on the map is probably close to the actual range of the species.

Material examined: 271 specimens.

443 *Lycaena phleas* Linnaeus(Linnaeus, 1761)
Four subspecies are recognized, only three of which are restricted to tundra habitat.
L. p. hypophleas Boisduval, 1852)
Type-locality: Sierra of California.
**L. p. arethusa* (Wolley-Dod, 1907)
Type-locality: Sheep River, 30 miles south west of Calgary, Alberta.
L. p. feildeni (M'Lachlan, 1878)
Type-locality: Ellesmere Island, 81° 41 N., North West Territories.

Notes. –

The distribution patterns and relationships between the various subspecies in Europe and North America are poorly understood. In North America, one subspecies, *L.p. americanaLycaena phleas americana*, does not occur on tundra. Also, while *L. p. arethusa* specimens are encountered most often above treeline, some range well below treeline in Alberta. The type locality, if taken literally, is well below treeline, although Wolley-Dod may have been referring to the headwaters of the River, which are much higher in elevation. Specimens have been taken below treeline more regularly at Mountain Park, and northwards on Prospect Mountain, and at Moberly Creek, and Grande Cache. In spite of intensive collecting in recent years, specimens have not been found below treeline south of Mountain Park. For this reason, boreo-montane populations are here considered to be derived from alpine populations, and this subspecies is considered a tundra butterfly. It is also possible that the low altitude populations represent a distinct taxon separate from the alpine populations.

Geographical Distribution. –

L. p. arethusa is found as far south as Colorado, and as far north as Grande Cache, Alberta. The nominotypical form is European. This species is found over much of Europe and Asia. The

Nearctic distribution is indicated in Figure 5. Alberta distribution is indicated in Figure 25.

Material examined: 33 specimens.

445 *Lyceana snowi* (Edwards, 1881)

Two subspecies are recognized.

* *L. s. snowi* (Edwards, 1881)

Type-locality: Colorado.

L. s. henryae (Cadbury, 1937)

Type-locality: Cariboo Pass, Peace River Country, British Columbia.

Notes. –

L. s. henryae has not been collected since its description. *L. s. snowi* was first collected in Alberta by T. E. Bean in the vicinity of Laggan. However, specimens are more commonly encountered to the south than to the north in the province. In Alberta, it appears to be restricted to above treeline, but in Wyoming, it has been reported below treeline (Howe, 1975; Ferris, 1971).

Opinions differ about the relationship of this species to *L. cupreus*, whose range is below treeline in California, north east to Colorado. Howe (1975) and Ehrlich and Ehrlich (1961) consider the two groups conspecific. Dos Passos and most previous authors consider them distinct. I follow dos Passos. Certainly the two taxa are closely related. However, this taxonomic problem does not affect the outcome of this project because the Alberta material is clearly similar to *L. snowi* of Colorado.

Geographical Distribution. –

Distribution is indicated in Figure 6. *L. snowi* is found from Colorado north to central British Columbia. It has not been reported from the Yukon Territory or Alaska. Alberta distribution is indicated in Figure 26.

Material examined: 25 specimens.

595 *Euphydryas editha* (Boisduval, 1852)

Eighteen subspecies are currently recognized. Of these, only four are restricted to tundra. These are treated below.

E. e. nubigena Behr, 1863

Type-locality: Headwaters of the Tuolumne River and beyond to elevations of 11500 ft. (3538 m.), California.

E. e. lawrenci Gunder, 1931

Type-locality: Mount Theilsen, Douglas County, Oregon.

E. e. colonia Write, 1905

Type-locality: Mt. Hood, Oregon.

**E. e. beani* Skinner, 1897

Type-locality: High elevations near Laggan, Alberta (Lake Louise).

Notes. –

While most subspecies of *E. editha* are not found on tundra, these four subspecies appear to be restricted to tundra environments, which they evidently colonized recently, apparently in response to empty niches on the mountains they inhabit. With the exception of *E. e. beani*, they occur where there are virtually no other tundra butterflies.

E. e. beani has been reported more commonly to the south of the type locality, where specimens were collected by T. E. Bean. Specimens are easily confused with alpine specimens

of *E. anicia*. The northern records of *E. e. beani* are older, and may represent misidentifications, but most of the southern records have been verified in recent years.

Geographical Distribution. –

Distributions are indicated in Figure 7. *E. e. beani* is restricted to the mountains of southern Alberta and British Columbia and *E. e. nubigena* is restricted to the high Sierras of California. The other two subspecies have only been recorded from their type localities. Alberta distribution is indicated in Figure 27.

Material examined: 27 specimens.

597 *Boloria napaca* (Hoffmansegg, 1804)

The nominotypical form is European. Four subspecies have been recorded from North America.

B. n. alaskensis (Holland, 1900)

Type-locality: Mountains between 40 mile and Mission Creeks, Alaska.

B. n. nearctica Verity, 1932

Type-locality: North eastern Alaska.

**B. n. reiffi* Reuss, 1925

Type locality: Mountains of British Columbia.

B. n. halli Klots, 1940

Type-locality: Green River Pass, Wind River Mountains, Wyoming.

Notes. –

Shepard (in Howe, 1975) has made *B. n. reiffi* a junior synonym of *B. n. alaskensis* . This is without warrant, for it is not based on study of the type specimen, but rather on conjecture by Klots (1940) and Warren (1944). Specimens of *B. n. reiffi* have been recorded from Kvass Creek Summit and the headwaters of the Berland River, Alberta. I adopt this assignment because of the proximity of the type locality.

In the past, these subspecies were treated under the name *B. pales* (Denis and Schiffermuller, 1775). Warren(1944) placed them under the name *B. napaea*. This is generally accepted, but it is based on characters of doubtful significance.

Geographical Distribution. –

Distribution is indicated in Figure 8. This species is common in arctic and alpine areas of Europe and Asia. In North America, it is found in Alaska, Yukon Territory, and arctic North West Territories excluding the northern-most arctic islands. It has been reported in northern British Columbia, and as disjunct populations in central Alberta, and in Wyoming. Alberta distribution is indicated in Figure 28.

Material examined: 78 specimens.

601 *Boloria improba (Butler, 1877)*

Two subspecies are recognized.

B. i. improba (Butler, 1877)

Type-locality: Winter Cove, Cambridge Bay, North West Territories.

**B. i. youngi* (Holland, 1900)

Type-locality: Mountains between 40 mile and Mission Creeks, Alaska.

Notes. –

B. improba was first reported from Alberta in 1976 from Prospect Mountain (see Figure 1). Eleven specimens have been collected. Adults of this population appear most similar to those of

B. i. youngi, and the Alberta population is so placed, but it may deserve subspecific status. Adults show constant and remarkably stable differences from adults of other examined populations. This is a highly variable species year to year, so longer series are needed before a decision can be made. In the summer of 1978, another disjunct population was discovered in Colorado (Sperling, pers. comm.)
This population has been described as *B. acrocnema* Gall and Sperling, 1980.

Geographical Distribution. –

Distributions of the two subspecies are indicated in Figure 9. This species is also known from arctic Europe and Asia. In North America, it is found in Alaska, the Yukon Territory, arctic North West Territories excluding the high arctic islands, northern British Columbia, and disjunct populations in west-central Alberta and Colorado. Alberta distribution is indicated in Figure 29.

Material examined 147 specimens.

604 *Boloria polaris* (Boisduval, 1829)
Three subspecies are recognized.
B. p. polaris (Boisduval, 1829)
Type-locality: Norwegian Alps.
B. p. groenlandica (Skinner, 1892)
Type-locality: Greenland.
B p. stellata Masters, 1972
Type-locality: Churchill, Manitoba.

Notes. –

Adults of this species are rarely collected, although they are often abundant. Unlike most butterfly species, very few infraspecific names have been proposed for this taxon.

Geographical Distribution. –

This species is found from Lappland across arctic Europe and Asia to Greenland. In North America, it is recorded from Alaska, Yukon Territory, North West Territories including the high arctic islands, Manitoba, Quebec, Labrador, and northern British Columbia. Distribution is indicated in Figure 10.

Material examined: 234 specimens.

606 **Boloria alberta* (Edwards, 1890)
Type-locality: Laggan, Alberta (Lake Louise).

Notes. –

This species has been reported from Anaktuvuk Pass, Alaska, but because worn adults of *B. polaris* and *B. distincta* resemble those of *B. alberta*, this record must be regarded as suspect.

Geographical Distribution. –

This species is restricted to high alpine areas in northern Montana, southern Alberta and British Columbia. A different subspecies has been reported from the U.S.S.R. Nearctic distribution is indicated in Figure 12. Alberta distribution is indicated in Figure 30.

Material examined: 43 specimens.

607 **Boloria astarte* (Doubleday, 1846-1852(1847))
Type-locality: Mountains of British Columbia, here restricted to Mt. Cheam.

Notes. –

dos Passos (1964) and Shepard (in Howe, 1975) recognize two subspecies; *B. a. astarte* and *B. a. distincta*. Wyatt (1957) discounts the hypothesis that they are conspecific. Because of numerous differences between the two taxa, I follow Wyatt. Certainly they are easily separated, but closely related. The problem does not affect the outcome of this project.

Type-locality is the mountains of British Columbia. (Edwards 1891) roposed the name which he later recognized as a junior synonym of *B. astarte*. The type locality for *A. victoria* is Laggan, Alberta (Lake Louise).

At the time of the description of *B. astarte*, British Columbia s boundaries were poorly defined or non-existent, and the area around Laggan was unexplored. It seems reasonable to restrict the type locality of *B. astarte* to the locality nearest the major cities of British Columbia around 1800-1820. The type-locality is hereby restricted to Mount Cheam, south of Hope, British Columbia, where lives the population closes to Vancouver Island and the mouth of the Frazer River.

Geographical Distribution. –

Distribution is indicated in Figure 12. This species is recorded from British Columbia, Alberta, and northern Washington and Montana. Alberta distribution is indicated in Figure 34.

Material examined: 60 specimens.

607b *Boloria distincta* (Gibson, 1920)

Type-locality: Harrington Creek, Yukon Territory.

Geographical Distribution. –

In North America this species appears to be restricted to Beringia with one record from Atlin, British Columbia and a few from the Richardson Mountains, North West Territories. Distribution is indicated in Figure 13.

Material examined: 15 specimens.

610 *Boloria eunomia* (Esper, 1787)

Seven subspecies are recognized in North America, four of which are restricted to tundra (includes alpine bogs) conditions above treeline.

B. e. caelestis (Hemming, 1933)

Type-locality: Hall Valley, Park County, Colorado.

B. e. ursadentis Ferris and Groothuis, 1971

Type-locality: Beartooth Plateau, Wyoming.

**B. e. nichollae* (Barnes and Benjamin, 1926)

Type-locality: Rocky Mountains of North America, here restricted to the north end of Wilcox Pass, Columbia ice fields, Jasper National Park, Alberta.

B. e. laddi (Klots, 1940)

Type-locality: Lewis Lake, Albany County, Wyoming.

Notes. –

B. e. nichollae was misidentified by Shepard (in Howe, 1975). His identification was based on the fact that according to the published itinerary of the original collector s trip west (Nicholls, 1905), she did not and could not have collected in the area where a dark form corresponding to the description is found. However, she made a later trip west, as indicated by records of *B. alberta* and *B. astarte* collected by her at the headwaters of the Saskatchewan and Athabasca Rivers, Alberta (Entomological Society of Ontario, records; seasonal collection list,

1907). This area is the center of the distribution of the dark form of *B. eunomia*. This suggests that Mrs. Nicholls could have collected the type series during her second trip. This is supported by a paratype from the USNM which is darker than normal adults from most areas in the mountains of Alberta. Accordingly, the type locality is restricted to the north end of Wilcox pass, Columbia Ice Fields, Jasper National Park, Alberta. This pass was chosen because before the highway was built between Jasper and Lake Louise, the only way to cross from the Athabasca watershed to that of the Saskatchewan River was via this pass by pack train (J. Pike, pers. comm.). If Mrs. Nicholls collected in both watersheds, she must have used this pass, and probably collected there as evidenced by the type series of *B. e. nichollae*.

Geographical Distribution. –

Distributions of the four subspecies are indicated in Figure 14. *B. e. nichollae* is restricted to west-central Alberta, *B. e. ursadentis* to its type-locality (Beartooth Plateau, Wyoming), *B. e. laddi* to Wyoming, and *B. e. caelestis* to Colorado. There has been one record of *B. e. laddi* from Colorado, but this has been questioned. Alberta distribution is indicated in Figure 32.

Material examined: 184 specimens.

667 *Oeneis bore* (Schneider, 1792)

Included here is *O. taygete* Geyer, 1830. Six subspecies are recognized.

O. b. taygete Geyer, 1830

Type-locality: Hopedale, Labrador.

O. b. gaspeensis dos Passos, 1949

Type-locality: Mount Albert, Quebec.

O. b. fordi dos Passos, 1949

Type-locality: Kuskoquim River Valley, Alaska.

**O. b. edwardsi* dos Passos, 1949

Type-locality: San Juan Mountains, Hinsdale County, Colorado.

O. b. hanburyi Watkins, 1928 .

Type-locality: Coronation Gulf, North West Territories.

O. b. mackinleyensis dos Passos, 1949

Type-locality: Mount McKinley National Park, Alaska.

Notes. –

Adults of these subspecies are very similar to one another. Alberta material was ascribed to *O. b. edwardsi* by dos Passos in his description. Adults were first collected in the province at Nordegg by K. Bowman.

Adults of what is usually considered *O. taygete* are distinguished by the presence of white outlined veins on the ventral hind wings. This character does not appear to be constant. Because of this, and the amount of confusion surrounding the use of these names in the literature, they are here treated as synonyms to facilitate the handling of locality data. Either way, the outcome of this project is not affected.

Geographical Distribution. –

Distribution is indicated in Figure 15. This species is found in Alaska, Yukon Territory, arctic North West Territories excluding the high arctic islands, Quebec, Manitoba, Labrador, northern British Columbia, Alberta, Montana, Wyoming, and Colorado. There is one record from Utah. It is also known from Europe and Asia, along the coast of the Arctic Ocean. Alberta distribution is indicated in Figure 32.

Material examined: 178 specimens.

670 *Oeneis melissa* (Fabricius, 1775)
Seven subspecies are recognized.
O. m. melissa (Fabricius, 1775)
Type-locality: Newfoundland.
O. m. semplei Holland, 1931
Type-locality: Little Cape James River; Churchill, Manitoba; Hudson Bay.
O. m. assimilis Butler, 1868
Type-locality: Repulse Bay, North West Territories.
O. m. gibsoni Holland, 1931
Type-locality: Kuskoquim River Valley, Alaska.
O. m. lucilla Barnes and McDunnogh, 1918
Type-locality: Hall Valley, Colorado.
**O. m. beani* Elwes, 1893
Type-locality: Laggan, Alberta (Lake Louise).
O. m. semidea (Say, 1828)
Type-locality: White Mountains, New Hampshire.

Notes. –

North of the type-locality, specimens of *O. m. beani*, while appearing phenotypically identical to southern specimens, live in a different habitat. Southern populations are restricted to areas of rock covered by black lichens. In the north, they are found on stable talus slopes where there is no black lichen.

Distributions of the seven subspecies are indicated in Figure 16. Geographical limits of the arctic subspecies are uncertain. This species is recorded from Alaska, the Yukon Territory, arctic North West Territories excluding the high arctic islands, Quebec, Manitoba, Labrador, Newfoundland, British Columbia, Alberta, Montana, Wyoming, Utah, Colorado, New Mexico, and New Hampshire. Alberta distribution is indicated in Figure 34.

Material examined: 99 specimens.

671 *Oeneis polixenes* (Fabricius, 1775)
Six subspecies are recognized.
O. p. polixenes (Fabricius, 1775)
Type-locality: Labrador? America Boreali
O. p. subhyalina (Curtis, 1835)
Type-locality: Boothia Peninsula, North West Territories.
O. p. katahdin (Newcomb, 1901)
Type-locality: Mount Katahdin, Maine.
O. p. peartiae (Edwards, 1897)
Type-locality: Winter Cove, Cambridge Bay, North West Territories.
**O. p. brucei* (Edwards, 1891)
Type-locality: Bullion Mountain, Hall Valley, Park County, Colorado.
O. p. yukonensis Gibson, 1920
Type-locality: unavailable.

Notes. –

There appears to be a gap in the distribution of *O. p. brucei*. It is not reported from Montana or southern Alberta. *O. b. edwardsi* shows a similar gap. These two species are very similar, and in both, adults fly early in the season. It is possible that this gap represents a temporal collecting bias, and not an actual disjunction.

O. p. brucei was first collected in Alberta in the vicinity of Banff. Adults are more commonly encountered north of Banff than south. This species has not been reported from southern British Columbia, being restricted, like *O. b. edwardsi*, to the front ranges east of the Rocky Mountain Trench.

Geographical Distribution. –

Distribution is indicated in Figure 17. This species has been reported from Alaska, the Yukon Territory, arctic North West Territories excluding the high arctic islands, Quebec, Manitoba, Labrador, northern British Columbia, Alberta, Wyoming, Colorado, and Maine. Alberta distribution is indicated in Figure 35.

Material examined: 283 specimens.

675 *Erebia magdalena* Strecker, 1880
Two subspecies are recognized.
E. m. magdalena Strecker, 1880
Type-locality: Mountains near Georgetown, Colorado.
E. m. mackinleyensis Gunder, 1932
Type-locality: Sable Pass, Mount McKinley National Park, Alaska.

Notes. –

In spite of intensive collecting, this species has not been reported from north of the Beartooth Plateau, Montana, or south of the Yukon Territory. The two subspecies are fairly distinct.

Geographical Distribution. –

Distribution is indicated in Figure 18. This species is known from Alaska, the Yukon Territory, Montana, Wyoming, Utah, Colorado, and New Mexico.

Material examined: 25 specimens.

676 *Erebia fasciata* Butler, 1868
Two subspecies are recognized
E. f. fasciata Butler, 1868
Type-locality: Victoria Island, North West Territories.
E. f. avinoffi Holland, 1930
Type-locality: Kotzebue Sound, Alaska.

Geographical Distribution. –

Neartic distribution is indicated in Figure 19. This species is known from Alaska, the Yukon Territory, and arctic North West Territories excluding the high arctic islands and Baffin Island. It is also recorded from Asia.

Material examined: 25 specimens.

677 *Erebia youngi* Holland, 1900
Three subspecies are recognized.
E. y. youngi Holland, 1900
Type-locality: Mountains between 40 mile and Mission Creeks, Alaska.

E. y. herscheli Leussler, 1935
Type-locality: Herschell Island, Yukon Territory.
E.y. rileyi dos Passos, 1947
Type-locality: Mount McKinley National Park, Alaska.

Notes. –

Adults of this species are easily confused with those of *E. dabanensis*; records of one may easily refer to the other.

Geographical Distribution. –

Distribution is indicated in Figure 20. This species is also recorded from Asia. In North America, it is found in Alaska, the Yukon Territory and western-most arctic North West Territories.

Material examined: 12 specimens.

Erebia dabanensis Erschoff, 1871
Type-locality: Chamar-daban, Urkutsk, U.S.S.R.

Notes. –

This species has tentatively been identified from a number of localities in Alaska. The specimens may represent *E. youngi*. Details for their separation are given in Warren (1936).

Geographical Distribution. –

Distribution is indicated in Figure 21. So far, this species has only been reported from Alaska and eastern Asia.

Material examined: 1 specimen.

Erebia inuitica Wyatt, 1966
Type-locality: Anaktuvuk Pass, Alaska.

Notes. –

This species has not been collected since its description.

Geographical Distribution. –

The type-locality is indicated in Figure 22.

681 *Erebia callias* Edwards , 1871
Type-locality: Colorado.

Notes. –

E. callias is common in the southern Rocky Mountains. It is the only endemic butterfly in the southern Rocky Mountains that is restricted to tundra.

Geographical Distribution. –

Distribution is indicated in Figure 23. It is recorded from Montana, Wyoming, Utah, and Colorado. It has also been reported from Asia.

Material examined: 23 specimens.

Twelve taxa are known from Alberta. Their distributions are shown in Figures 24 through 35. These taxa are:

C. n. streckeri Figure 24
L. p. arethusa Figure 25
L. s. snowi Figure 26
E. e. beani Figure 27
B. n. reiffi Figure 28
B. alberta Figure 30
B. astarte Figure 31
B. e. nichollae Figure 32
O. b. edwardsi Figure 33
O. m. beani Figure 34

B. i. youngi Figure 29 *O. p. brucei* Figure 35

These twelve taxa are grouped into four types of distribution patterns: Southern Montane, Central Montane, Disjuncts, and Endemics.

TYPE 1 - Southern Montane (Figure 36a)

This pattern includes five taxa whose ranges extend from Alberta south to the Montana-Wyoming border, or beyond to Colorado and New Mexico.

L. p. arethusa *O. b. edwardsi*
O. p. brucei *O. m. beani*
L. s. snowi

TYPE 2 - Central Montane (Figure 36b)

This group includes four taxa not found north of the British Columbia-Yukon Territory border, or south of northern-most Montana and Washington.

C. n. streckeri *B. alberta*
E. e. beani *B. astarte*

TYPE 3 - Disjuncts (Figure 36c)

One taxon found in Alberta represents a disjunction from a northern population. There do not appear to be any disjunctions from southern populations.

B. i. youngi

TYPE 4 - Endemic forms (Figure 36d)

Included here are two taxa known only from the central Canadian Rocky Mountains.

B. e. nichollae *B. n. reiffi*

Possibly three other taxa may be placed here. As mentioned earlier, the Alberta population of *Boloria improba* may represent an undescribed subspecies. Also, *O. m. beani* from around Prospect Mountain shows an ecological specialization which may deserve recognition, and the one specimen of *L. p. arethusa* from above treeline at Prospect Mountain is very different from normal *arethusa*. This may be an aberration, or it may represent an undescribed taxon.

DISCUSSION

In general, distribution patterns are determined in part by ecological tolerances, or proximal factors, and in part by past events, or historical factors (Udvardy, 1969; Larsen and Barry, 1974; Löve and Löve, 1974). I have not attempted to study explicitly by experimental means those factors involved with ecological tolerance. Rather, I accept that such exist, and assume that the tundra butterflies of Alberta exist in such areas because the latter are favorable. Further, I assume that these taxa do not live elsewhere in geographically proximal areas, because they cannot tolerate other ecological conditions, either biotic or physical. I concentrate on explaining the historical concomitants of the distribution patterns.

In general, historical explanations depend on a series of hypotheses, because the determining events were not observed, and thus their existence and interrelations must be inferred from evidence that is presently available. However, meaningful inferences cannot be generated *in vacuo*. Rather, they are based on assumptions that must be regarded, for the sake of a given set of circumstances, as axiomatic. My assumptions are as follows.

1. Climatic events of the Wisconsin glacial stages influenced the distribution patterns of extant butterfly taxa of tundra areas of Alberta. There is a vast amount of data which document the effects of this glaciation on other groups of animals and plants. For the

present, these effects are assumed for the tundra butterflies as well. Specific indications derived from distribution patterns shown by tundra butterflies are discussed in the section on source areas of this fauna.

2. Unglaciated areas of the eastern slopes of the Rocky Mountains were habitable during glacial times.

   This assumption is necessary to explain the presence of disjunct populations of non-butterfly taxa in the study area, given that these disjunctions are not artifacts and are interpreted correctly. Geological data (Roed, Mountjoy, Rutter, 1967; Rutter, 1972; Boydell, 1972; Curry, 1976; Reimchen and Bayrock, 1977; Stalker, 1977; Alley, 1973; Jackson, 1977; Reeves, 1973) indicate the likelihood that this assumption is valid.

3. Immediate ancestral stocks of all species of butterflies that are included in each distribution type survived together in the same refugium.

   This assumption is required to explain the fact that more than one taxon shows a given distribution pattern.

4. Dispersal of tundra adapted stocks has been slow and orderly. This has been the result of the non-random and gradual retreat of Wisconsin ice sheets. Because life spans are short, and flight capabilities are generally poor, tundra butterflies do not appear to be suited to dispersal over long distances.

5. Evidence of endemism is evidence of isolation of such stocks from other populations for a period of time that extends from the present to at least the end of the Sangamon interglacial stage.

Genetic change usually requires a period of isolation (see Morisset, 1971, and Packer, 1971, for discussions in the context of endemism and refugia). Endemism is one way that such genetic change is expressed. The end of the Sangamon interglacial is the last possible time that endemic populations could have been genetically continuous with ancestral populations of other forms.

Explanation of the distribution patterns of the tundra butterflies of Alberta requires postulation of source areas of these populations. There are three potential source areas: Beringia, Continental North America south of Wisconsin ice, and one or more refugia within the limits of continental ice along the Rocky Mountains in Alberta and British Columbia. Two are external to Alberta: Beringia, and Continental North America south of Wisconsin ice. One includes the eastern slopes of the Rocky Mountains, that is, an internal refugium in the sense that it was probably surrounded by ice at the height of the Wisconsin glacial stage.

Existence of the external source areas is well established by an abundance of evidence. Existence of the internal source area is based on less extensive evidence: at least twelve plant taxa have disjunct populations in the front ranges of the Rocky Mountains (Packer and Vitt, 1974) as do three species of beetles (Belicek, 1976; Ball, pers. comm.), and one crustacean. The endemic species of crustacean which has been reported (Clifford and Bergstrom, 1976) is of questionable value in this context.

Extensive areas surrounded by ice were probably available in Alberta during Wisconsin time for habitation, although much of the unglaciated area was likely bedrock, and probably too rugged and too high to support tundra vegetation. Today, distribution of disjunct taxa is concentrated along the front ranges of the Rocky Mountains, and especially in the Mountain Park area. Endemic taxa are also centered in this area. Possibly the refugium was located in this area during the Wisconsin stage.

Figure 37 indicates the approximate limit of Wisconsin ice in the Mountain Park area. A high ridge on the western side, which now forms the Jasper National Park boundary, would have prevented ice from entering this area from the west. The northern boundary has been documented as Cordilleran ice in the Athabasca River Valley which coalesced with laurentide ice in the vicinity of Hinton (Roed, Mountjoy, and Rutter, 1967) See Figure 5. The eastern boundary would most likely have been somewhere in the foothills, or the eastern slopes of Cadomin and Red Cap Mountains. The southern boundary is uncertain, and the refugium may have extended south to Nordegg, where ice in the Saskatchewan River Valley would have formed a barrier. The area encompassed is a series of valleys and ridges which run in an east-west direction. They provide, at present, considerable and varied alpine habitat. All ice present in the refugium during Wisconsin time would have been thin and of local derivation. It is probable that small pro-glacial lakes were present during the height of glaciation, being formed by summer melt waters off the ice and from annual snow fall. Alpine tundra could have maintained an extent and position similar to that at present.

Of the three possible source areas listed above, I believe that only two contained immediate ancestors of the extant populations under consideration. My major hypotheses, then, are:

1. The source area for butterflies with distribution types 1 and 2 was an external refugium south of the ice.
2. The source area for butterflies with distribution types 3 and 4 was an internal, or Albertan refugium.

Each of these hypotheses is discussed below. Additionally, a series of secondary hypotheses is presented in conjunction with locating more precisely the source area of the butterflies from the external refugium south of Wisconsin ice.

The source area of the nine taxa in groups 1 and 2 is placed south of Wisconsin ice for the following reasons.

Of the nine species involved, five also live in Beringia, and are represented there by distinctive forms. Alberta material is easily allied with southern forms in all five species. None of the Beringian forms even approach the Alberta border to the north.

The remaining four species are not in Beringia, and two have clear relationships with southern taxa. This suggests that they evolved south of the Wisconsin ice sheets.

No tundra butterflies in Beringia have dispersed south into and still survive in Alberta.

In the Trichoptera (Nimmo, 1971) and Coccinellidae (Belicek, 1976) faunas that have been investigated, only a very small proportion has been derived from Beringia. This includes all habitat types. Of all Alberta s butterflies, the source area of only one can be identified as Beringia. This suggests that not only tundra elements, but all elements of the Beringian fauna could not easily migrate south, including the boreal forest communities.

If these taxa survived Wisconsin glaciations in the Alberta refugium, there are a number of indications that might be expected.

First, we might expect that some of these taxa would have dispersed north from the refugium as well as south. There would not be barriers to entry into Alaska for the four species not present there now. We would also expect that some of the distinctly alpine taxa would be found on arctic tundra in the North West Territories. These possibilities have not been realized. It is possible that some of these taxa survived in the Alberta refugium, but have not contributed to colonization of other areas, however, in the absence of endemic tendencies, these cannot be identified.

It is also unlikely that taxa surviving in the Alberta refugium could have dispersed as far as New Mexico in post-glacial times, but not into the coastal ranges of Washington, Oregon, and California. This would imply long distance dispersal between mountain ranges, and the gaps in habitat are similar in size on both the eastern and western mountain ranges.

In order to locate the source area of types 1 and 2 more precisely, the following hypotheses are made.

1. Taxa in types 1 and 2 survived the Wisconsin glaciation in the same refugium.
2. Dispersal south into Wyoming and Colorado from this refugium was blocked by gaps in habitat.
3. The tundra belt south of the ice sheet was very narrow and broken. This prevented dispersal east to New England and Quebec.
4. Dispersal west and south along the coastal ranges was blocked by large gaps in habitat in central Washington.

These hypotheses are discussed below.

1. Taxa in types 1 and 2 survived together.

   These taxa have similar boundaries on three sides of their present ranges. This indicates that they are responding to retreat of Wisconsin ice in a similar manner. If so, it is reasonable to expect that they would respond to the Wisconsin ice advances in a similar manner as well, and that as they were displaced south, and northern colonies were extinguished, the surviving colonies would be found in about the same area.

   Type 1 distributions have been identified in plants (Packer and Vitt, 1974), Trichoptera (Nimmo, 1971), and Coccinellidae (Belicek, 1976). Type 2 distributions have been identified in Trichoptera (Nimmo, 1971), but not in plants or Coccinellidae. At least one species of carabid beetle shows this type of distribution: *Nebria schwarzi*. This indicates a fairly general phenomenon, and that large elements of the tundra community were involved. This is to be expected if the hypothesis is correct.

2. Dispersal from this refugium south was blocked by gaps in habitat.

   This hypothesis is necessary to explain the fact that type 2 taxa have not dispersed farther south, where there appears to be ample suitable habitat, and empty niches available. Because there are no plant taxa which show this type of distribution, these butterfly taxa are not limited by foodplant distribution. It would seem that they have been physically blocked from dispersing south. The only reasonable explanation is that tundra was not very extensive, and that these taxa are not capable of crossing even minor gaps in habitat. In other words, dispersal can only be accomplished if the habitat is continuous. By hypothesizing a narrow tundra belt, breaks would occur in the belt in the vicinity of central Montana, which is where the barrier seems to have been.

   Also in support of this hypothesis is the fact that the two endemic taxa in the southern Rocky Mountains have not been able to disperse north across this barrier.

   It would appear that the presence of type 1 taxa in the southern Rocky Mountains would weaken this argument. However, because two of these taxa are derived from non-tundra species which evolved below the ice margin, their presence probably dates to pre-Wisconsin times. Also, because the three species on isolated tundra in New England and Quebec are also in the Rocky Mountains, they must either be capable of much better dispersal, or they must have had more time to reach these areas. While they may be more efficient at dispersing than other tundra butterflies, they have not managed to invade the arctic islands very successfully, which weakens the suggestion that they extended their

ranges into the southern Rocky Mountains in post-Wisconsin times.

If they were present in North America during earlier, more extensive glaciations, not only would the extent of tundra be greater, and therefore the gaps smaller, but they would have had considerably more time to spread through the southern Rocky Mountains. It is suggested, therefore, that these taxa represent elements of an older dispersal south, perhaps during Illinoisan or Nebraskan glaciations. This might also explain the presence of *E. magdalena* and *E. callias* in Colorado and Wyoming.

3. The tundra belt along the southern margin of Wisconsin ice was discontinuous.

Six of the nine species under discussion are not represented in the isolated tundra of New England and Quebec. The three tundra species there are represented by subspecies that are more closely related to subspecies in Labrador and the eastern arctic. This indicates that a major barrier was present. Because the six species that are absent inhabit a variety of habitats, and two of them inhabit all tundra areas except New England, Quebec, and the southern Rocky Mountains, it is reasonable to expect that the nature of this barrier had to be a break in the tundra belt. Otherwise, at least one or two of these species would be expected on the tundra in New England and Quebec, and the relationship would be closer between eastern and western populations of the three species found on both sides of this barrier.

Based on pollen core data, similar conclusions have been reached with respect to the discontinuous tundra belt (Löve, 1959; Ritchie, 1969; Wright, 1970).

4. Dispersal west and south along the coastal ranges was blocked by large gaps in habitat in central Washington.

Only two of the twelve species in Alberta are also on the coastal ranges, where each is represented by a different subspecies. Tundras from Oregon south to the Sierra Nevada are the most depauperate in terms of tundra butterflies, in North America. This indicates a major barrier. If minor barriers prove to be effective for these butterflies, distances between the mountain peaks in Oregon and southern Washington would be almost insurmountable. This is in keeping with the suggestion that the nine taxa in types 1 and 2 are unable to cross unfavorable habitat, and necessitates only one assumption to explain all boundaries and barriers encountered in this study.

It appears that tundra plants are also reacting to this barrier. According to Billings (1974), only 20% of the flora of the tundra of the Sierra Nevada has affinities with northern and arctic tundra floras. Of all known tundra in North America, this, and that of the Great Basin, are the most depauperate in arctic-alpine species.

The hypothesis seems to explain all the available data, while being contradicted by none. As more groups are investigated, particularly Carabidae, and the infraspecific relationships in the flora between the tundra areas discussed above, further tests of the hypothesis can be made.

The probable extent of the external refugium is indicated in Figure 43.

Before an attempt is made to locate the source area for butterflies with distribution types 3 and 4, it is necessary to discuss the assumptions that the distributions known for these taxa are accurate.

The only taxon that shows a clear disjunction is *B. improba youngi*, which is represented in Alberta by a population disjunct from arctic Canada and Alaska. Collecting in the gap has been minimal, so there is a possibility that this disjunction is an artifact, in which instance, this would represent the only dispersal into Alberta from the north in Post-glacial times. Because of the phenotypical differences between the Prospect Mountain population and the populations in

the north, and because this species has not been found on the mountains in the vicinity of Prospect Mountain, I suspect that it probably represents a real disjunction. This would indicate either long distance dispersal, or survival in the area during the Wisconsin. Because of the distances involved (over 600 km.) it is unlikely that this represents long range dispersal. Adults of this species are very weak fliers. The presence of a disjunct population in Colorado supports the hypothesis that this species has a relict distribution in the Rocky Mountains, and that this distribution is in part due to Wisconsin events.

Two taxa in type 4 may represent endemic forms. *B. e. nichollae* is very distinctive. *B. n. reiffi* is largely unknown. The type specimen appears to have been lost, and no specimens have been found that fit the type description. Alberta material has not been studied. A short series from Pink Mountain, British Columbia has not been examined because of lack of material from the Yukon Territory and Alaska for comparison. This species must have been present before the Wisconsin glaciations because there is one disjunct population in Wyoming which represents a different subspecies.

The only feasible explanation for the presence of types 3 and 4 distributions is that these taxa survived at least the Classical Wisconsin glaciation in the Alberta Refugium.

Barriers to dispersal appear to be either lack of suitable habitat, or selection against dispersal during glaciations. This has been suggested for Carabidae (Lindroth, 1949).

Colonization of present day tundra in Alberta

In this section I will discuss the contribution and dispersal routes from each of the two refugia into Alberta tundra.

Dispersal of taxa which survived Wisconsin glaciations in the Alberta refugium has been minimal. *B. e. nichollae* has dispersed west and south to areas within a 40 km. radius of Prospect Mountain, *B. n. reiffi* and *B. i. youngi* are now located to the north of the refugium, which may indicate Post-glacial dispersal, or possibly that the refugium extended north of the Athabasca River Valley as a series of broken nunataks. If the ecological form of *O. m. beani* found in this area survived in the refugium, it has dispersed about the same amount as *B. e. nichollae*. This refugium does not seem to have contributed much to the colonization of Alberta tundra in Post-glacial times.

With respect to the external refugium, as Wisconsin ice retreated, the tundra south of the ice is expected to have followed the ice margins north. As the tundra moved northward, the tundra butterflies would have as well. Boreal forest following behind the tundra would first invade valleys, gradually isolating pieces of tundra on mountains. With the continued movements of both communities north, these isolated tundras would slowly move up the mountains to the summits as conditions for tree growth improved lower down. As ice retreated still farther, Laurentide ice withdrew to the east across northern Alberta and what is now the barrenlands of the North West Territories. The tundra belt followed the ice movements and boreal forest eventually replaced tundra in all the mountain valleys creating a series of isolated tundra communities on mountain summits. The breakup of continuous tundra in the mountains effectively halted the dispersal north of tundra butterflies. The migration of the biota in this refugium is summarized in Figure 38.

Because Cordilleran ice in northern British Columbia and the Yukon Territory did not break up until well after Laurentide ice had retreated eastward, Beringian flora and fauna were blocked from dispersing south by the presence of intact tundra and boreal forest communities derived from south of the ice sheets. In other words, the Beringian communities were blocked

first by ice barriers, and later, by inter and intra specific competition.

CONCLUSIONS

Two Wisconsin butterfly refugia can be identified in the Rocky Mountains of Alberta and adjacent areas. The first, Mountain Park, did not have a significant role in re-colonizing Alberta after the ice retreated. The second, northern Washington, Idaho, and Montana, was an important dispersal center for butterflies. Tundra butterflies are the only direct living indication that the tundra belt south of the ice margin was not continuous.

This suggests that the tundra butterfly fauna has an important potential as an indicator of refugia, and should be investigated whenever a study on the location of a refugium is undertaken.

The importance of refugia is twofold. They serve as centers of dispersal, and as centers for the development of new taxa. This study also suggests that large refugia tend to act as centers of dispersal, and that small refugia tend to serve as centers for the development of new taxa.

Where areas surrounded by ice have been identified by geologists, evidence which indicates refugia has usually been found by biologists, but geologists cannot determine the limits of a given community type within the boundaries of an open, or continental refugium. Only investigation of the biological components can determine these limits with accuracy.

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REFERENCES

Alley, N.F. 1973. Glacial stratigraphy and the limits of the Rocky Mountain and Laurentide ice sheets in southwestern Alberta; Canada. Bulletin of Canadian Petroleum Geology 21; 153–177.

Bang-Haas, O. 1927. citation not found.

Barnes, W. and McDunnough, J.H. 1918. Contributions to the natural history of the Lepidoptera of North America 4(2):61–208. plates xi-xxv. The Review Press, Decatur, Illinois.

Barnes, W. and Benjamin, F.H. 1926. Notes on the diurnal Lepidoptera, with additions and corrections to the recent List of diurnal Lepidoptera . Bulletin of the Southern California Academy of Sciences 25(3): 88–98.

Behr, H. 1863. On California Lepidoptera. Proceedings of the California Academy of Sciences 3(1): 84–93.

Belicek, J. 1976. Coccinellidae of western Canada and Alaska. M.Sc. thesis, Department of Entomology, University of Alberta, Edmonton. 408 pages.

Billings, W.D. 1974. Adaptations and origins of alpine plants. Arctic and Alpine Research 6(2): 129–142.

Boisduval, J.B. 1828. Europaeorum Lepidoptororum Index Methodicus. Paris. Méquignon-Marvis. 103 pages.

Boisduval, J.B. 1829-1834. Histoire General et incongraphie des Lepidopteres et des chenilles de l Amerique Septentrionale. Paris. Roret. 228 pages, 71 plates.

Boisduval, J.B. 1832. Supplément à l histoire naturelle des Lepidopteres d Europe. Paris. Mequignon-Marvis. vol. 1, Diurnes, 25 pages, 50 plates.

Boisduval, J.B. 1852. Lepidopteres de la California. Annales de la Societe Entomologique de France. Ser. 2; 275–324.

Boydell, A.N. 1972. Multiple glaciations on the foothills, Rocky Mountain House area, Alberta. Ph.D. Thesis, Department of Geography, University of Calgary, Calgary. 137 pages.

Boydell, A.N., Bayrock, L.A. and Reimchen, T.H. 1974. Surficial geology of the Rocky Mountain House area, Alberta. Map. 1:250,000. Alberta Research Council.

Butler, A.G. 1868. A catalogue of diurnal Lepidoptera of the family Satyridae in the collection of the British Museum. 8 volumes, 211 pages.

Butler, A.G. 1877. Description of a new species of *Argynnis* from arctic America. The Entomologist s Monthly Magazine 13(153):206.

Cadbury, J.W. 1937. Lepidoptera collected in northern British Columbia by Miss Josephine de N. Henry. Part 1. Rhopalocera. Proceedings of the Academy of Natural Sciences, Philadelphia. vol. 89; 387-413.

Clifford, H.F., and Bergstrom, G. 1976. The blind aquatic isopod *Salmasellus* from a cave spring of the Rocky Mountains eastern slopes, with comments on a Wisconsin refugium. Canadian Journal of Zoology 54(11):2028–2032.

Curry, D.V. 1976. Hydrogeology of the Tri-creek basin, Alberta. Research Council of Alberta Bulletin 33. 67 pages.

Curtis, J. 1835. Descriptions of the insects brought home by J.C. Ross. in J.C. Ross. Narrative of a second voyage in search of a north west passage. Appendix, pages 59–80.

Denis, M. and Schiffermuller, I. 1775. Systematisches Verzeichniss der schmetterlinge der Wiener gegend. 322 pages.

dos Passos, C.F. 1947. The distribution of *Oeneis taygete* Geyer in North America with descriptions of new subspecies (Lepidoptera; Satyridae). American Museum Novitates 1399. 21 pages.

dos Passos, C.F. 1949. New butterflies from Mount McKinley National Park, Alaska, with a revision of *Erebia rossii* (Rhopalocera, Satyridae). American Museum Novitates 1389. 17 pages.

dos Passos, C.F. 1964. A synonymic list of the nearctic Rhopalocera. Lepidopterists Society Memoirs 1. v and 145 pages.

Doubleday, E. and Hewitson, W. 1847 (1846-1852). The genera of diurnal Lepidoptera comprising their generic characters, a notice of their habits and transformations, and a catalogue of the species of each genus; illustrated with 86 coloured plates from drawings by W.C. Hewitson. Longman. London. 250 pages, 30 plates.

Edwards, H. 1881. On two new forms of the genus *Parnassius*. Papilio 1: 2–4.

Edwards, W.H. 1870. Descriptions of new species of diurnal Lepidoptera found within the United States. Transactions of the American Entomological Society 3: 10–22.

Edwards, W.H. 1871. Descriptions of new species of North American butterflies. Transactions of the American Entomological Society 3: 266–277.

Edwards, W.H. 1881. Description of a new species of *Chrysophanus*. Transactions of the Kansas Academy of Sciences 7: 69–70.

Edwards, W.H. 1890. Description of a new species of *Argynnis* from Canada. Canadian Entomologist 22(6): 113–114.

Edwards, W.H. 1891. Description of a new species of *Erebia*, and notes on the so called *Chionobas bore* of Colorado, Canadian Entomologist 23: 31–33.

Edwards, W.H. 1891b. Description of a new species of *Argynnis* from Alberta Territory. Canadian Entomologist 23: 198–199.

Edwards, W.H. 1887-1897(1895). The butterflies of North America. 3. American Entomological Society. Boston. 51 pages.

Gall, L. and Sperling, F. 1980. A new high altitude species of the Genus *Boloria* from southwestern Colorado (Nymphalidae), with a discussion of Phenetics and hierarchical decisions. Journal of the Lepidopterists Society 34(2): 230–252.

Ehrlich, P.R. 1956. Problems of arctic-alpine distribution as illustrated by the butterfly genus *Erebia* (Satyridae). Proceedings of the 10th International Congress of Entomology. vol. 1; 683–686.

Ehrlich, P.R. and Ehrlich, A. 1961. How to know the butterflies. Wm. C. Brown Co., Dubuque, Iowa. 262 pages.

Elwes, H.J. and Edwards, J. 1893. A revision of the genus *Oeneis*. Transactions of the Entomological Society of London 1893; 457–481.

Entomological Society of Ontario Report. 1907. Notes on Captures. pages 118–133.

Erschoff, N.G. 1871. Diagnoses de quelques especes nouvelles de Lepidopteres appartenant a la faune de la Russie Asiatique. Horae Societatis Entomologicae Rossicae 8; 315–318.

Esper, E.J.C. 1787(1799). Die schmetterlinge in abbildungen nach der natur mit beschreibungen. Supplemenband Theils l. Erlangen, Walther. 120 pages.

Fabricius, J.C. 1775. Systema entomologiae sistens insectorum classes, ordines, genera species, adjectis synonymis locis descriptionibus, observationibus. Flensburgi et Lipsiae, Korte. 832 pages.

Ferris, C.D. 1971. An annotated checklist of the Rhopalocera (butterflies) of Wyoming. University of Wyoming Science Monograph 23. 79 pages.

Ferris, C.D. and Groothius, D.R. 1971. A new subspecies of *Boloria eunomia* (Nymphalidae) from Wyoming. Journal of Research on the Lepidoptera 9(4): 243–248.

Ford, E.B. 1946. Butterflies. Collins. London 368 pages.

Freeman, T.N. 1956. The distribution of arctic and subarctic butterflies. Proceedings of the 10th International Congress of Entomology. vol. 1; 659–672.

Gall, L. and Sperling, F. 1980. A new high altitude species of the Genus *Boloria* from southwestern Colorado (Nymphalidae), with a discussion of Phenetics and hierarchical decisions. Journal of the Lepidopterists Society 34(2): 230–252.

Geyer, C. (1827-1838) 1830. in Hübner, J. Sammlung Exotischer Schmetterlinge. Augsburg. vol. 3. 53 pages.

Gibson, A. 1920. The Lepidoptera collected by the Canadian arctic expedition 1913-1918. vol. 3: insects. part 1; Lepidoptera, pages 1i-58i.

Grote, A. 1875. The effect of the glacial epoch upon the distribution of insects in North America. Canadian Entomologist 7; 164–167.

Grum-Grschimailo, G.F. 1895. Lepidoptera palaearctica nova 3. Horae Societatis Entomologicae Rossicae xxix; 290–293.

Guenee, A. 1864. Note sur quelque especes du genre *Colias*. Annales de la Societe Entomologique de France. 4e ser. vol. iv; 197–200.

Gunder, J.D. 1931. Some new butterflies (Lepid; Rhopalocera). Bulletin of the Southern California Academy of Sciences 30; 45–48.

Gunder, J.D. 1932. New Rhopalocera (Lepidoptera). Canadian Entomologist 64; 276–284.

Hemming, F. 1933. Holarctic butterflies: miscellaneous notes on nomenclature. The Entomologist 66; 275–279.

Hoffmansegg, J.C. 1804. Alphabetisches verzeichness zu J. Hubner s abbildungen der papilionen mit den beigefugten vorzuglichsten symonymen. Illiger magazin fur Insectenkund 3; 181–206.

Holland, W.J. 1898. The butterfly book. Doubleday Page and Co. Garden City, New York. xx and 392 pages. 42 plates.

Holland, W.J. 1900. Alaskan insects. Entomologist s News 11(3): 381-389, 416–423.

Holland, W.J. 1930. New species of *Erebia* (Lepidoptera, Satyridae). Transactions of the American Entomological Society 66; 149–153.

Holland, W.J. 1931. Notes on some American butterflies mainly relating to classification and nomenclature. parts 2 and 3. Annals of the Carnegie Museum 20; 39–55.

Hovantiz, W. 1955. *Colias nastes* and *Colias hecla* from the Meade River, Alaska. Wasmann Journal of Biology 13; 1–8.

Howe, W.H. 1975. The butterflies of North America. Doubleday and Co., Inc. Garden City, Long Island. New York. 663 pages, 97 plates.

Jackson, L.E., Jr. 1977. Quaternary stratigraphy and terrain inventory of the Alberta portion of the Kananaskis Lakes 1:250,000 sheet (82-J). Ph. D. Thesis. Department of Geology, University of Calgary, Calgary. 480 pages.

Klots, A.B. 1940. New butterfly subspecies from Wyoming (Nymphalidae, Pieridae). American Museum Novitates 1054. 6 pages.

Klots, A.B. 1951. Holarctic butterfly speciation and subspeciation, especially in North America. The Lepidopterist s News 5(3-5): 24–27.

Klots, A.B. 1956. Southern extensions of arctic and subarctic insects in bogs and alpine areas. Abstract. Proceedings of the 10th International Congress of Entomology vol. 1; 711.

Larsen, J.A. and Barry, R.G. 1974. Paleoclimatology. pages 253–276 in J.D. Ives and R.G. Barry (eds.). Arctic and alpine environments. Methuen and Co. Ltd. London. 999 pages.

Leusler, R.A. 1935. Notes on the diurnal Lepidoptera of the Canadian arctic collected by Owen Bryant in teh summers of 1929 to 1932 with introduction and field notes by Owen Bryant. Bulletin of the Brooklyn Entomological Society 30; 42–62.

Lindroth, C.H. 1949. Die Fennoskandischen Carabidae. ein teirgeographische studie. Kungl. Vetenskpas-och Vitterhets Samhalle Handlingar. vi ser. B 4. no. 5. 911 pages.

Linnaeus, C. 1761. Systema naturae, sive regna tria naturae systematice proposita per classes, ordines, genera, species cum characteribus differentiis, synonymis, locis, ed. decima reformata. 11th edition. Holmiae, Magdeburgicae. 824 pages.

Löve, D. 1959. The postglacial development of the flora of Manitoba; a discussion. Canadian

Journal of Botany 37; 547–585

Löve, D. 1970. Subarctic and subalpine: where and what? Arctic and Alpine Research 2(1):63–73.

Löve, A. and Love, D. 1974. Historical plant geography A. Origin and evolution of the arctic and alpine floras, pages 571–604, in J.D. Ives, and R.G. Barry (eds.). Arctic and alpine environments. Methuen and Co. Ltd. London. 999 pages.

Masters, J.H. 1972. A new sub-species of *Boloria polaris* from Canada (Lepidoptera, Nymphalidae). The Entomologist s Record 84; 176–179.

Maynard, C.J. 1886. The butterflies of New England, with original descriptions of 106 species 40, iv and 65 pages. Boston, Mass.

M Lachlan, R. 1878. Report on the Insecta (including Arachnida) collected by captain Feilden and Mr. Hart between the parallels of 78° and 83° north latitude during the recent arctic expedition. Journal of the Linnaean Society xiv; 98–122.

Morriset, P. 1971. Endemism in the vascular plants of the gulf of St. Lawrence region. Le Naturaliste Canadien 98(2): 167–177.

Nicholls, 1905. Butterfly collecting in Canada, 1904. Report of the Entomological Society of Ontario 1905; 70–79.

Nimmo, A.P. 1971. The adult Rhyacophilidae and Limnephilidae (Trichoptera) of Alberta and eastern British Columbia and their post-glacial origin. Quaestiones Entomologicae 7(1): 3–234.

Newcomb, H.H. 1901. *Chionobas katahdin* and an account of its discovery. Entomological News xii; 206, 225–230.

News of the Lepidopterists Society, Field season summary 1974. #2. 20 pages.

News of the Lepidopterists Society, Field season summary 1975. #2. 20 pages.

News of the Lepidopterists Society, Field season summary 1976. #2. 20 pages.

Packer, J.G. 1971. Endemism in the flora os western Canada. Le Naturaliste Canadien 98(2): 131–144.

Packer, J.G. and Vitt, D.H. 1974. Mountain Park: a plant refugium in the Canadian Rocky Mountains. Canadian Journal of Botany 52; 1393–1409.

Prest, V.K. 1969. Retreat of Wisconsin and recent ice in North America. Geological Survey of Canada Map 1257 A.

Reeves, B.O.K. 1973. The nature and age of the contact between the Laurentide and Cordilleran ice sheets in the western interior of North America. Arctic and Alpine Research 5(1): 1–16.

Reimchen, T.H. and Bayrock, L.A. 1977. Surficial geology and erosion potential. Rocky Mountains and the foothills of Alberta. 183 pages and maps. Open File Report, Alberta Research Council, 77–14.

Reuss, T. 1925. *Boloria reiffi* Spez. Geogr. Nov. Internationale Entomologische Zeitschrift 19(36):279–180.

Ritchie, J.C. 1969. Absolute pollen frequencies and C-14 age of a section of holocene lake sediment from the Riding Mountain area of Manitoba. Canadian Journal of Botany 47; 1345–1380.

Roed, M.A., Mountjoy, E.W., and Rutter, N.W. 1967. The Athabasca valley erratics train, Alberta, and Pleistocene ice movements across the continental divide. Canadian Journal of Earth Science 4; 615–632.

Rutter, N.W. 1972. Geomorphology and multiple glaciation in the area of Banff, Alberta.

Geological Survey of Canada Bulletin 206, 54 pages.

Ryan, J.K. 1977. Energy Flow through arctic invertebrates at Truelove lowland, Devon Island, N.W.T., 75° 40 N 84° 40 W. Ph.D. Thesis. Department of Entomology, University of Alberta, Edmonton, 239 pages.

Say, T. 1828. American entomology, or descriptions of the insects of North America; illustrated by coloured figures from original drawings executed from nature. vol. 3. 112 pages. Philadelphia Museum.

Schneider, D.H. 1792. Neustes Magazin fur Liebhaber der Entomology. vol. 2, pages 128–256; vol. 3, pages 257-384; vol. 4, pages 386–512.

Skinner, H. 1897. Notes on Rhopalocera, with descriptions of new species and varieties. Canadian Entomologist 29; 154–156.

Skinner, H., and Mengal, L.W. 1892. Greenland Lepidoptera. Proceedings of the Academy of Natural Sciences, Philadelphia 1892; 156–159.

Stalker, A. McS. 1977. The probable extent of Classical Wisconsin ice in southern and central Alberta. Canadian Journal of Earth Science 14; 2614–2619.

Stanford, R.E. 1977. Rocky Mountain butterfly distribution maps. Denver, Colorado. 39 Denver, Colorado. 39 pages.

Strecker, F.H. 1880. Descriptions of some new species and varieties of North American Lepidoptera. Bulletin of the Brooklyn Entomological Society 3; 33–36.

Udvardy, M.D.F. 1969. Dynamic Zoogeography. Van Nostrand Reinholt Co. New York. xviii and 445 pages.

Verity, R. 1911. citation not found.

Verity, R. 1932. Notes on the geographical variations and evolution of *Boloria pales* Schiff. Iris, Dresden. 46; 101–109.

Warren, B.C.S. 1936. Monograph on the genus *Erebia*. Adlard and Son, Ltd. London. 407 pages, 104 plates.

Warren, B.C.S. 1944. A review of the classification of the Argynnidi; with a systematic revision of the genus *Boloria* (Lepidoptera: Nymphalidae). Transactions of the Royal Entomological Society of London 94:1–101, 46 plates.

Watkins, H.T.G. 1928. New satyrid butterflies. Annals and Magazine of Natural History series 10, vol. 1; 615–618.

Wolley-Dod, F.H. 1907. Notes on *Chrysophanus Hypophleas* and its allies, with description of a new species. Canadian Entomologist 39; 169-171.

Wright, H.E. Jr. 1970. Vegetational history of the Great Plains. pages 157–212 in Dort, W. Jr. and J.K. Jones Jr. (eds.) Pleistocene and Recent environments of the central Great Plains. Department of Geology, University of Kansas Special Publication 3. 433 pages.

Wright, W.G. 1905. The butterflies of the west coast of the United States; San Francisco. Entomologists News 16; 336–340.

Wyatt, C.W. 1957. Observations on *Boloria distincta* (Nymphalidae). Lepidopterists News 11(4-5):142–146.

Wyatt, C.W. 1966. Zeitschrift Wien Entomologische Gesellschaft 51; page 93. citation not found.

Wynne-Edwards, V.C. 1937. Isolated arctic and alpine floras on eastern North America: a discussion of their glacial and recent history. Royal Society of Canada: Proceedings and Transactions: Transactions 28, section 5; 33–58.

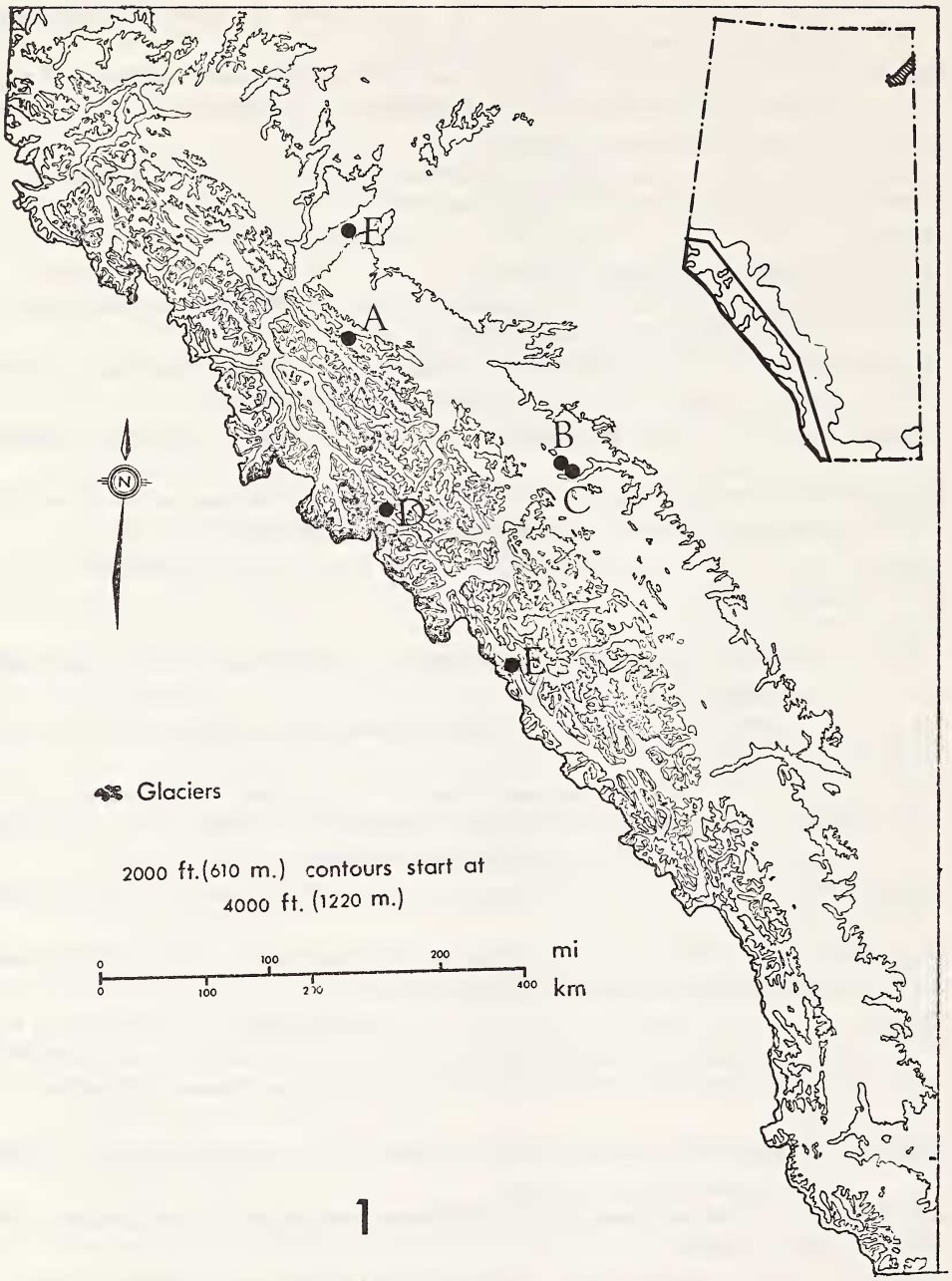


Fig. 1. Important localities mentioned in the text.
A–Prospect Mountain (Mountain Park); B–Shunda Mountain; C–Coliseum Mountain; D–Wilcox Pass; E–Laggan (Lake Louise); F–Hinton.

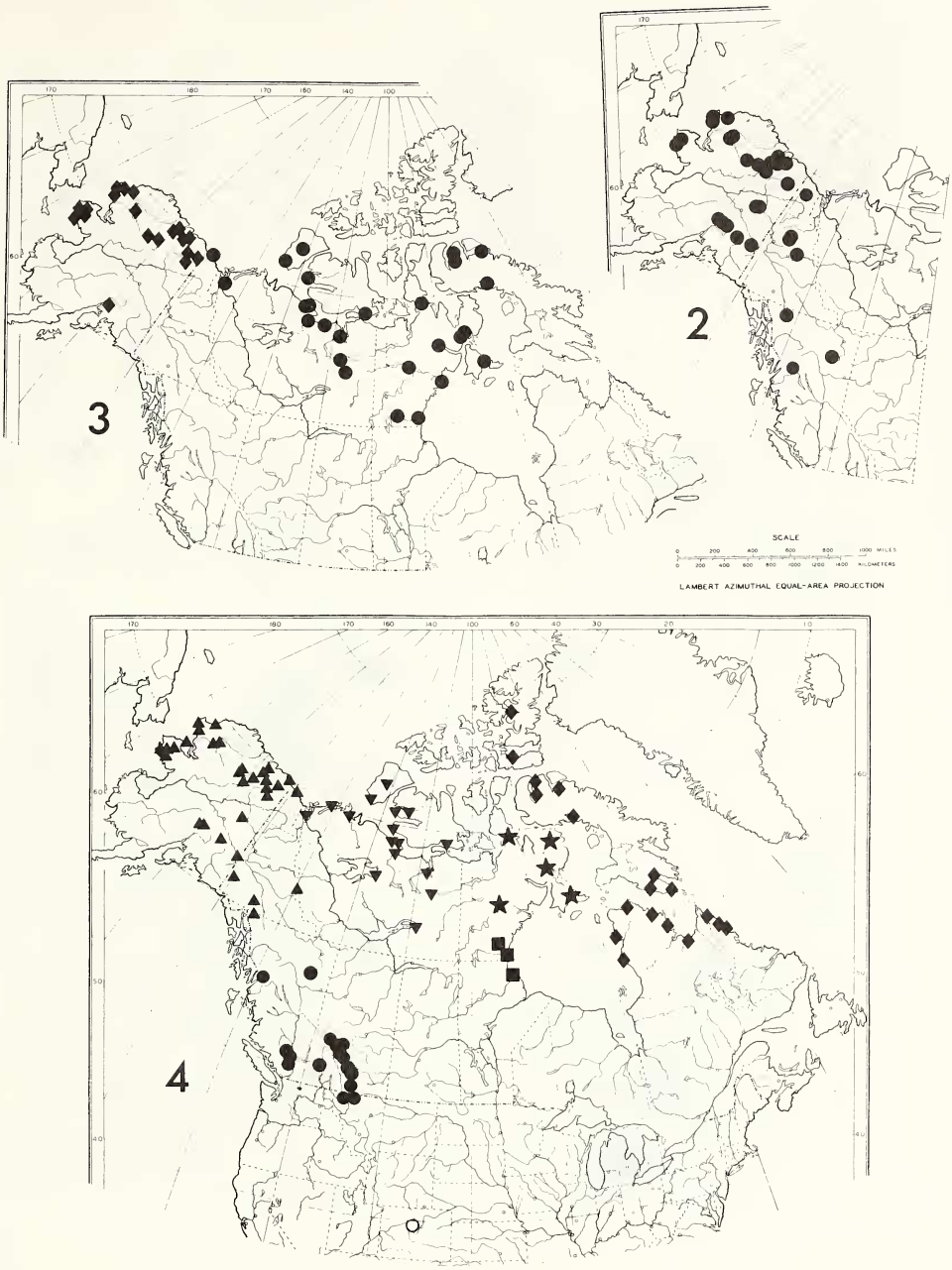
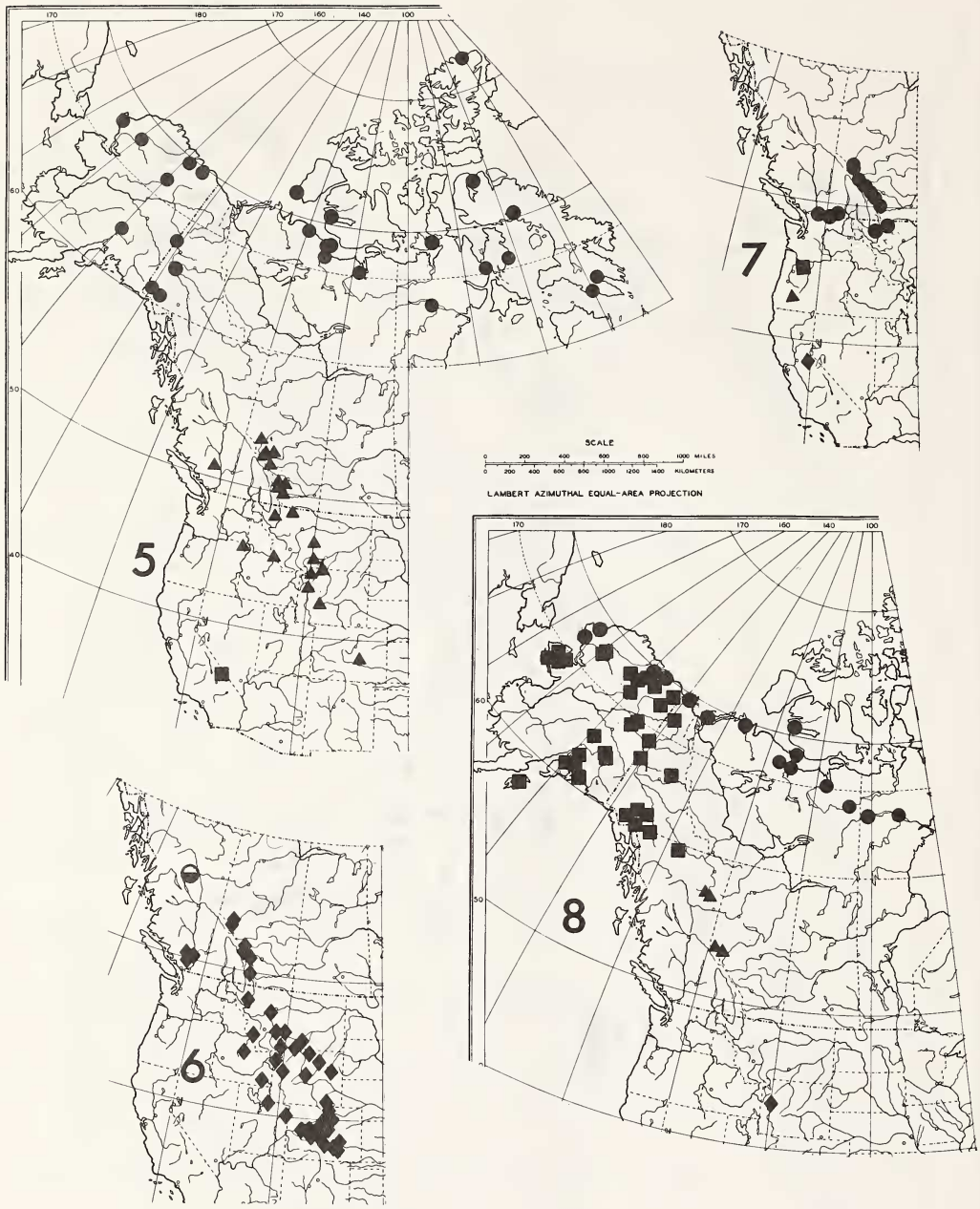
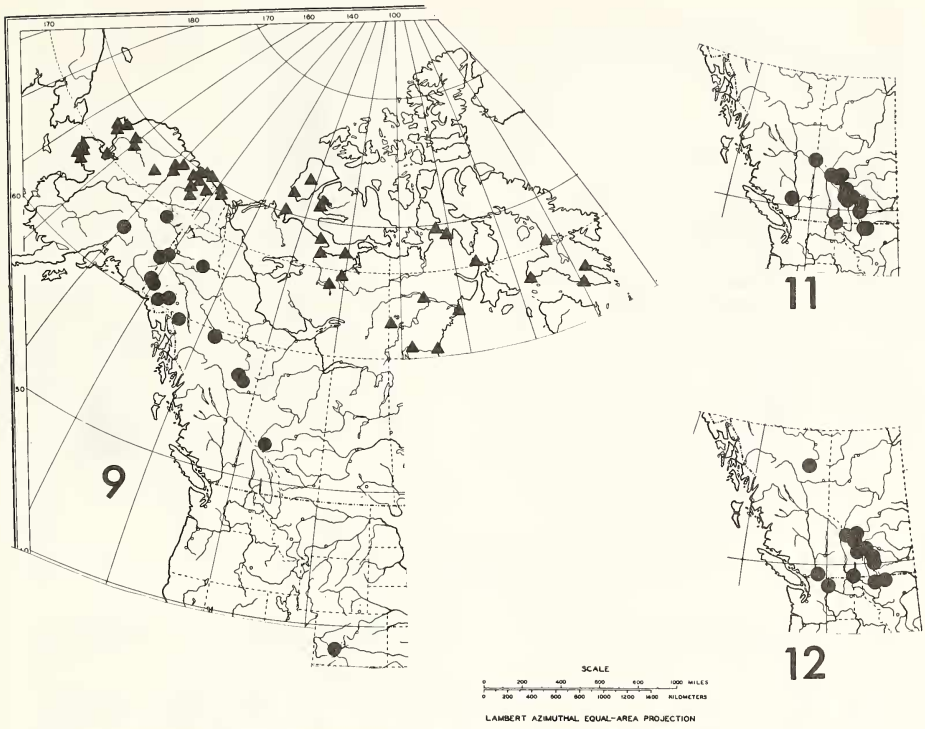


Fig. 2–4. Distribution of butterfly species and subspecies in North America.
Fig. 2. *Parnassius eversmanni thor.* Fig. 3. ● *Colias boothii;* ◆ *C. nastes thula.* Fig. 4. ◆ *Colias n. nastes;* ★ *C. n. rossii;* ■ *C. n. moina;* ● *C. n. streckeri;* ▼ *C. n. cocandicides;* ▲ *C. n. aliaska* unverified record. See Fig. 3 for range of *C. n. thula.*



Figs. 5–8. Distribution of butterfly species and subspecies in North America.
Fig. 5: ●*Lycaena phlaeas feildeni*; ▲*L. p. arethusa*; ■*L. p. hypophlaeas*. Fig. 6: ◆*Lycaena s. snowi*; ⊖*L. s. henryae*. Fig. 7: ●*Euphydryas editha beani*; ◆*E. e. nubigena*; ■*E. e. colonia*; ▲*E. e. lawrenci*. Fig. 8: ■*Boloria napaea alaskensis*; ●*B. n. nearctica*; ▲*B. n. reiffi*; ◆*B. n. halli*.



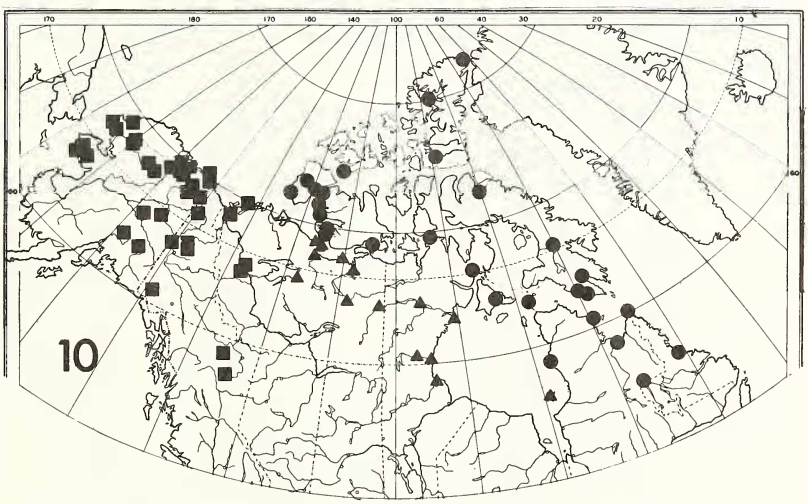


Fig. 9–12. Distribution of butterfly species and subspecies in North America.
Fig. 9: ▲ *B. i. improba;* ● *B. i. youngi.* Specimens from the locality in Colorado have been described as *B. acrocnema* Gall and Sperling, 1980. Fig. 10: ■ *Boloria p. polaris;* ● *B. p. groenlandica;* ▲*B. p. stellata;* identification uncertain. Fig. 11: *Boloria alberta;* Fig. 12: *Boloria astarte.*

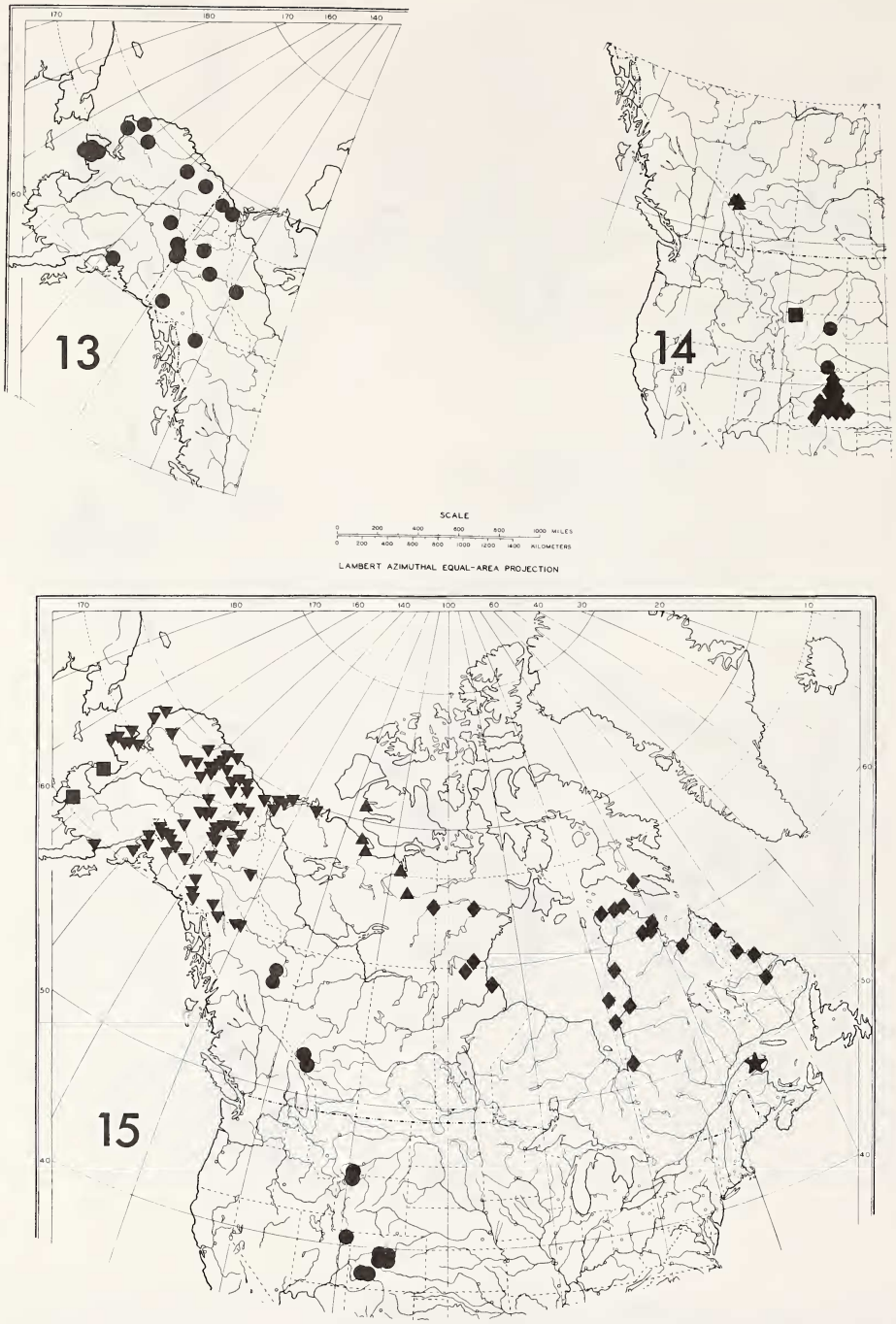
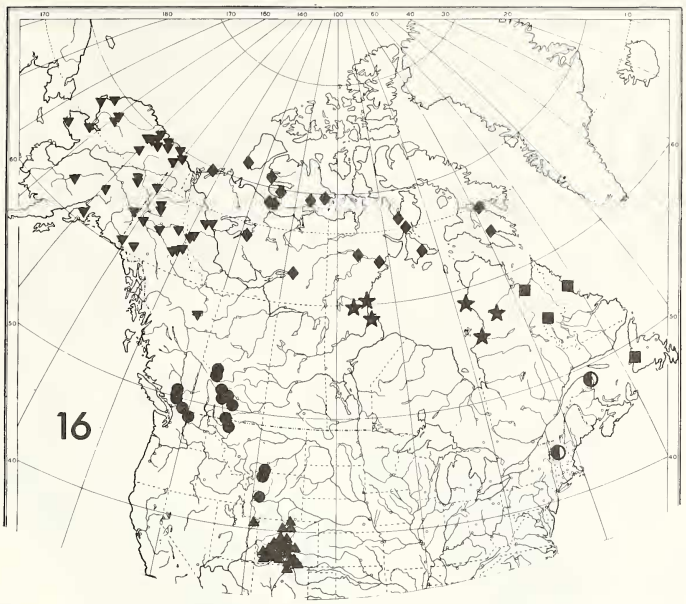
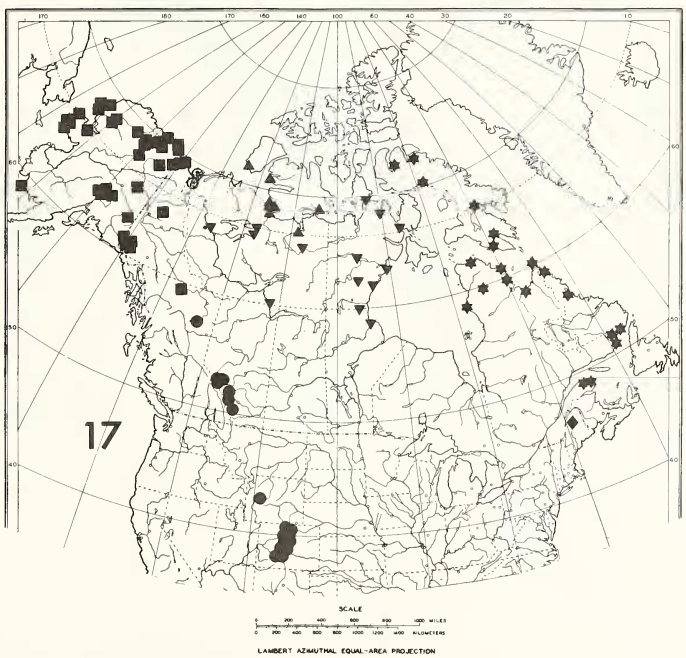
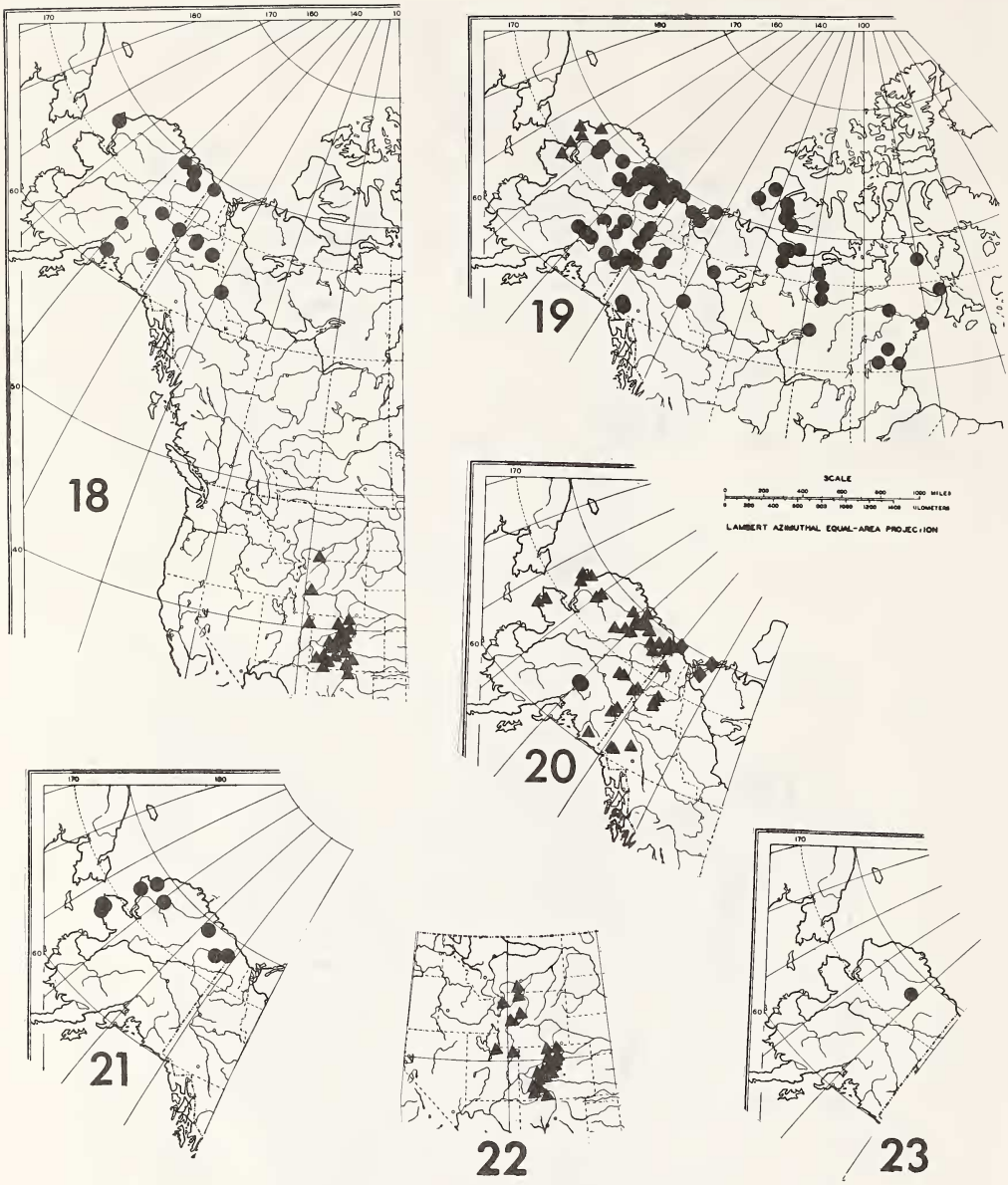


Fig. 13–15. Distribution of butterfly species and subspecies in North America.
Fig. 13: *Boloria distincta.* Fig. 14: ▲ *Bolaria eunomia nichollae;* ■ *B. e. ursadentis;* ● *B. e. laddi;* ◆ *B. e. caelestis.* Fig. 15: ◆ *Oeneis bore taygete;* ★ *O. b. gaspeensis;* ■ *O. b. fordi;* ● *O.b. edwardsi;* ▲ *O. b. hanburyi;* ▼ *O. b. mackinleyensis.*

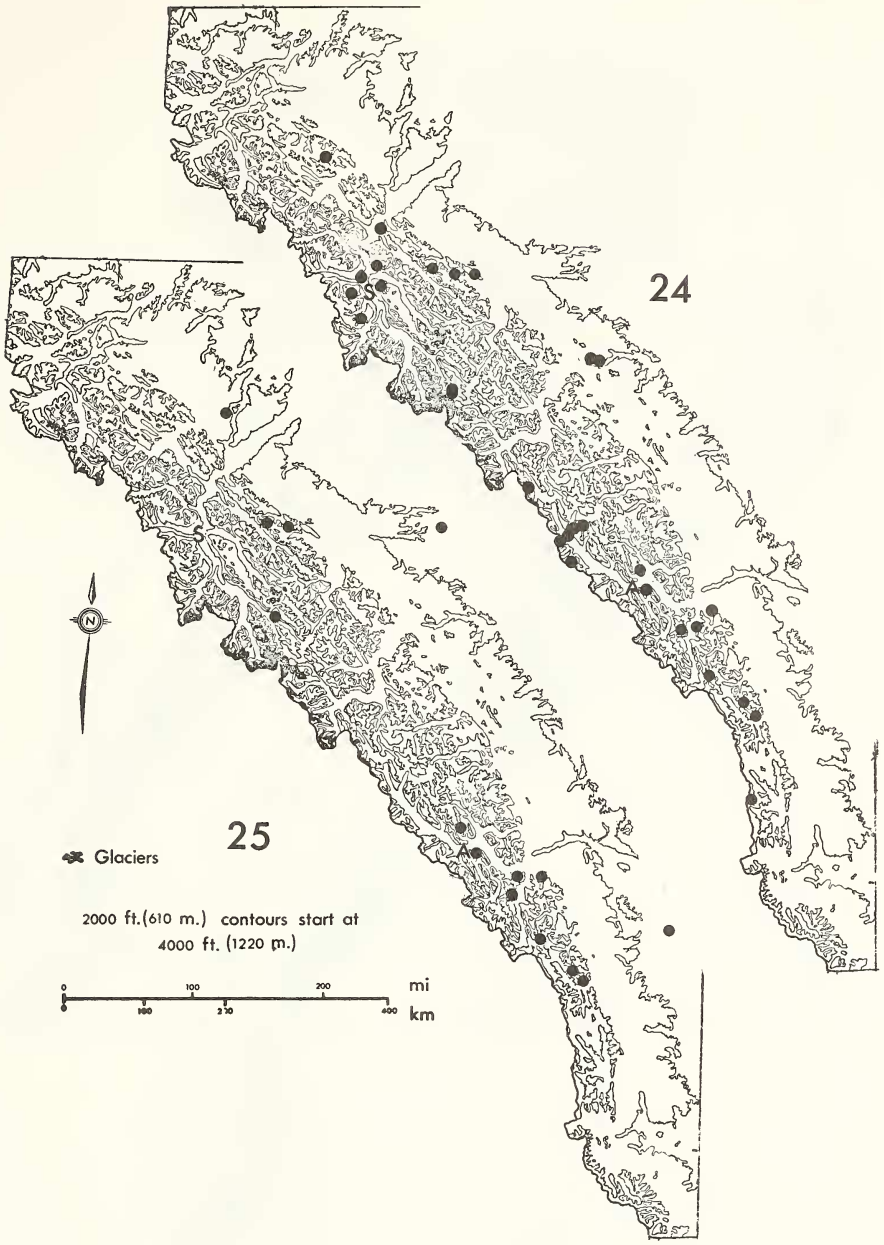




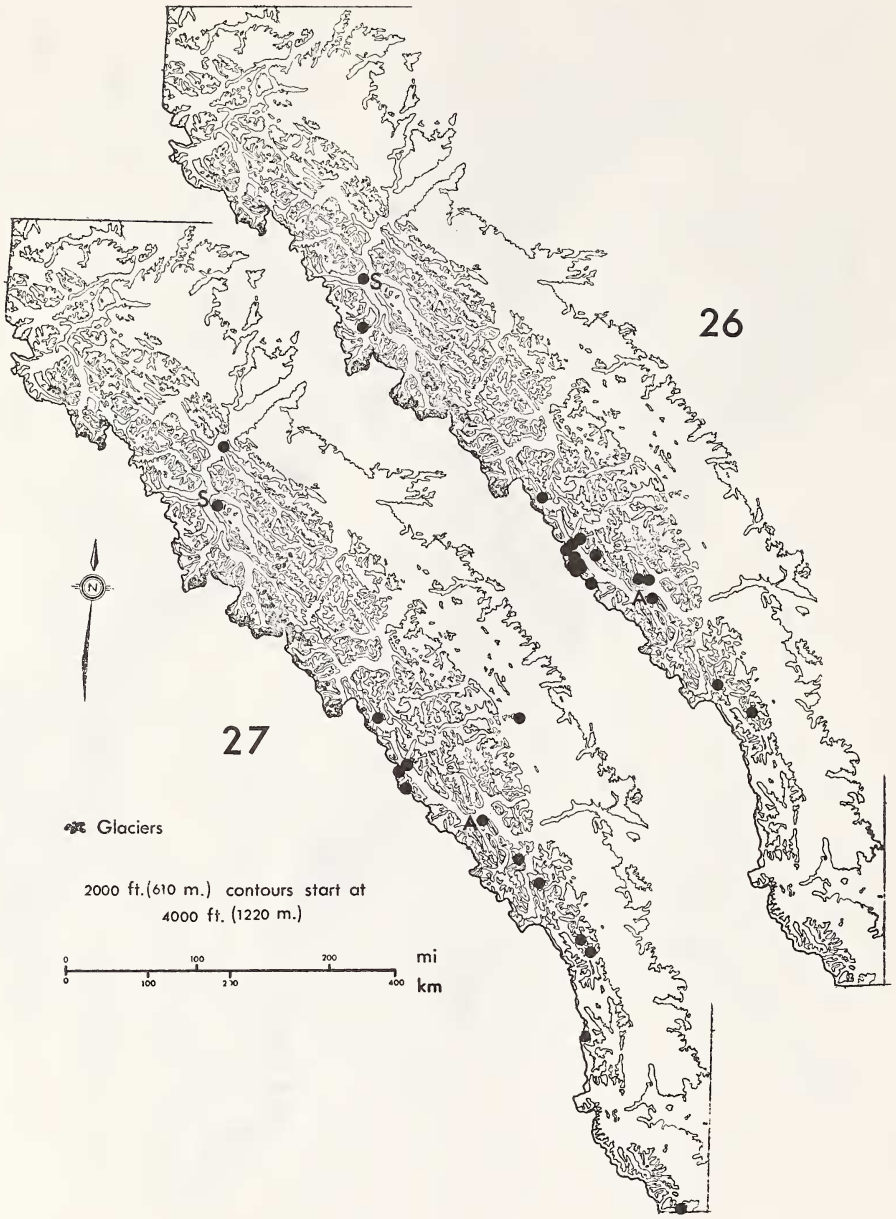
Figs. 16- 17. Distribution of butterfly species and subspecies in North America.
Fig. 16: ■*Oeneis m. mellissa;* ★*O. m. semplei;* ◆*O. m. assimillis;* ▼*O. m. gibsoni;* ▲*O. m. lucilla,*●*O. m. beani;* ◐*O. m. semidea.* Fig. 17: ★*O. p. polixenes;* ▼*O. p. subhyalina;* ◆*O. p. katahdin;* ▲*O. p. peartiae,*●*O. p. brucei;* ■*O. p. yukonensis.*



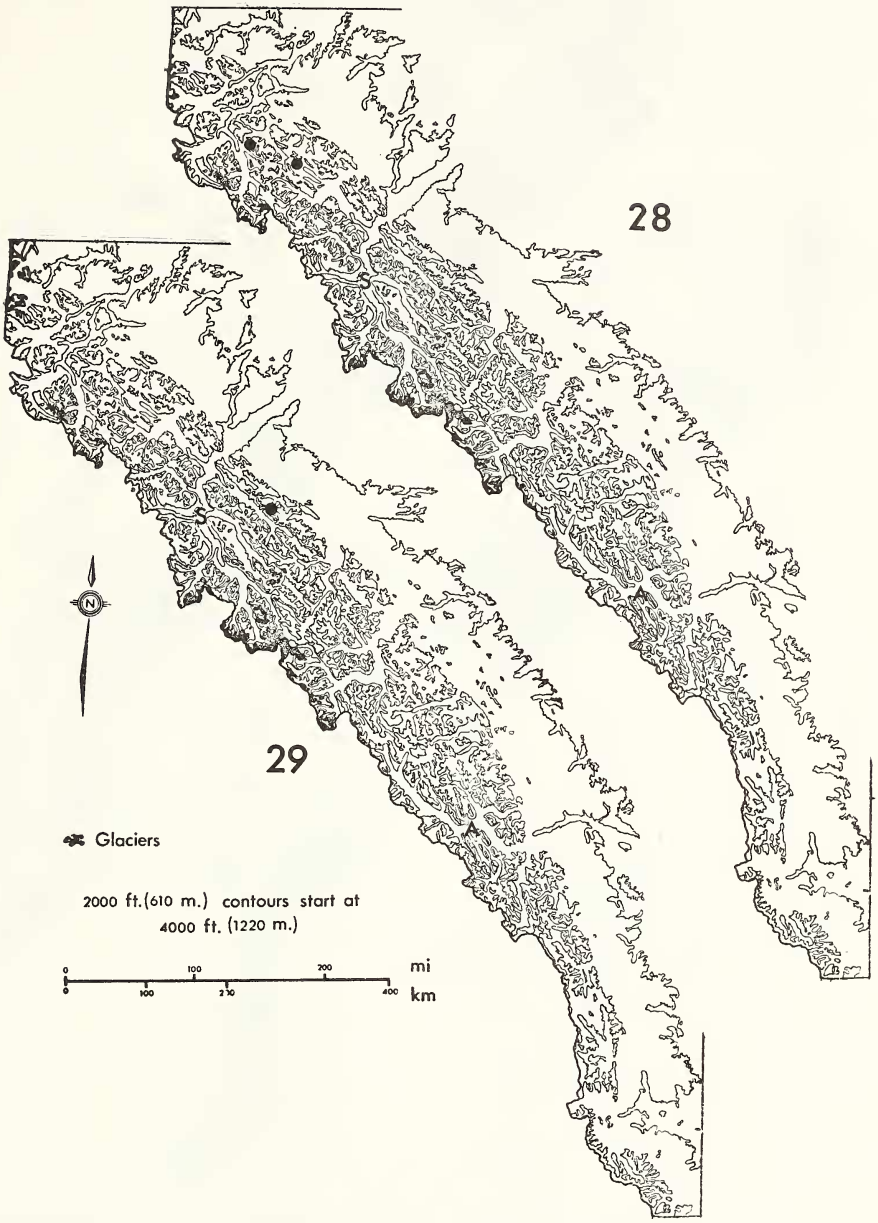
Figs. 18–23. Distribution of butterfly species and subspecies in North America.
Fig. 18: ▲*Erebia m. magdalena;*●*E. m. mackinleyensis. Fig. 19:*●*Erebia f. fasciata;* ▲*E. f. avinoffi.* Fig. 20: ▲ *Erebia y. youngi;* ◆*E. y. herscheli;*●*E. y. rileyi.* Fig. 21: *Erebia dabanensis.* Fig. 22: *Erebia callias.* Fig. 23: *Erebia inuitica.*



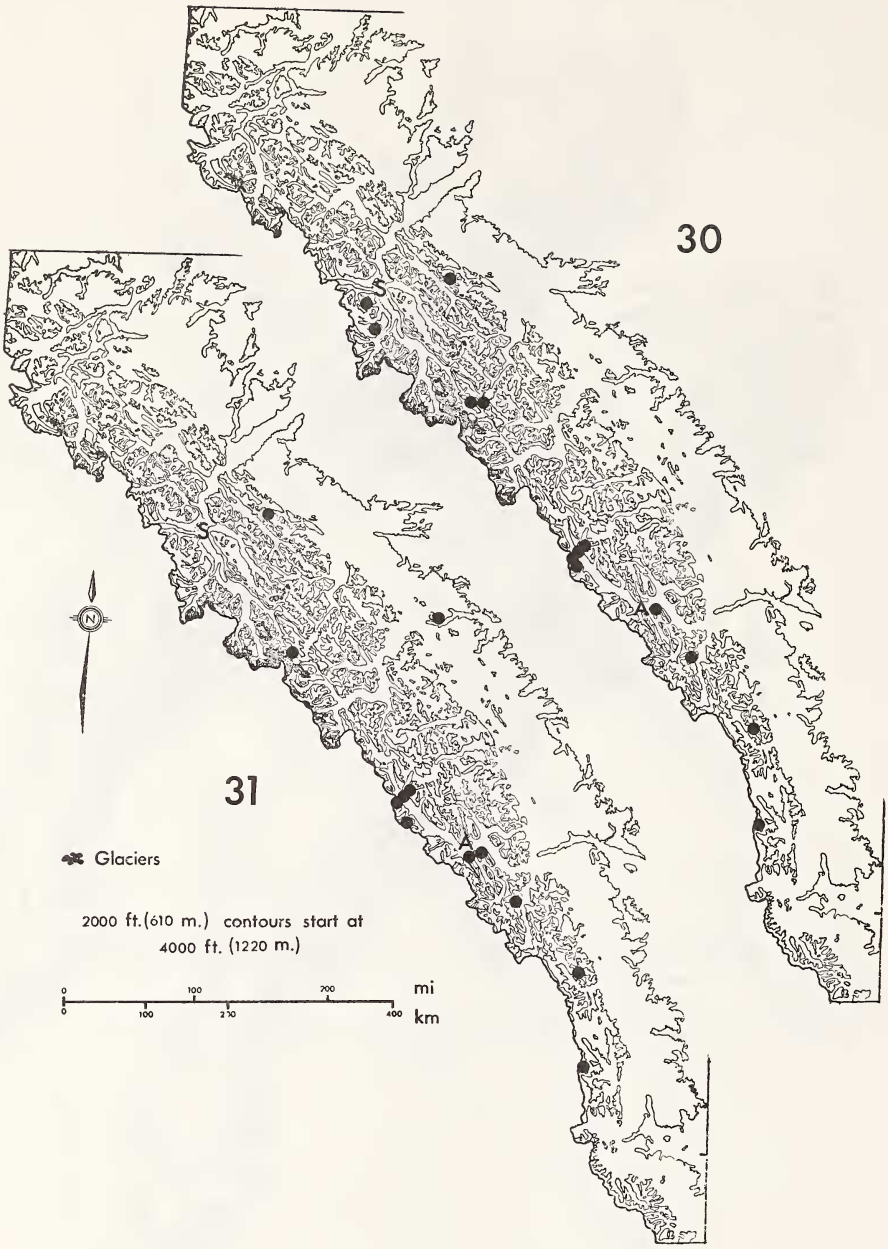
Figs. 24–25. Distribution of butterfly subspecies in Alberta.
A–Banff; S–Jasper. Fig. 24: *Colias nastes streckeri*. Fig. 25: *Lycaena phleas arethusa*.



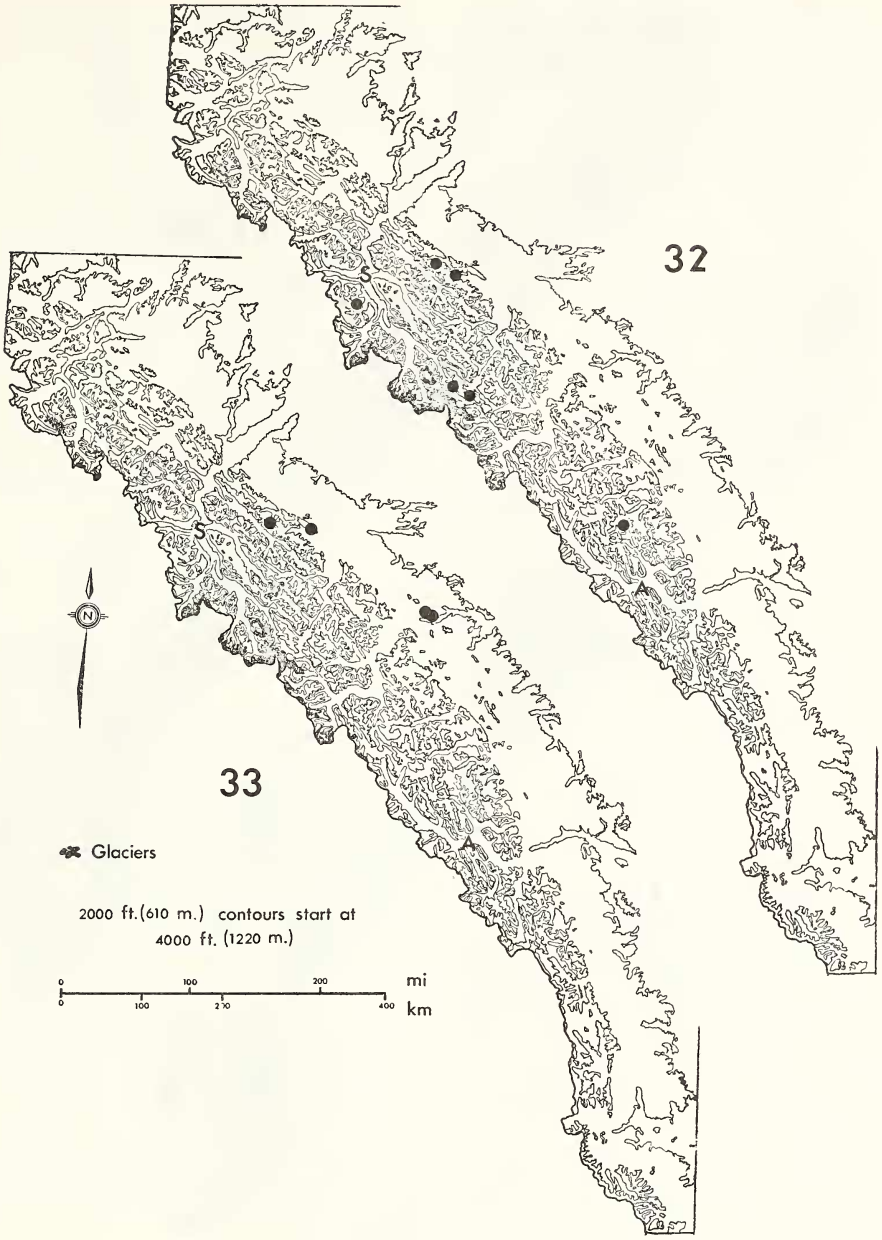
Figs. 26–27: Distribution of butterfly subspecies in Alberta.
A–Banff; S–Jasper. Fig. 26: *Lycaena s. snowi*. Fig. 27: *Euphydryas editha beani*.



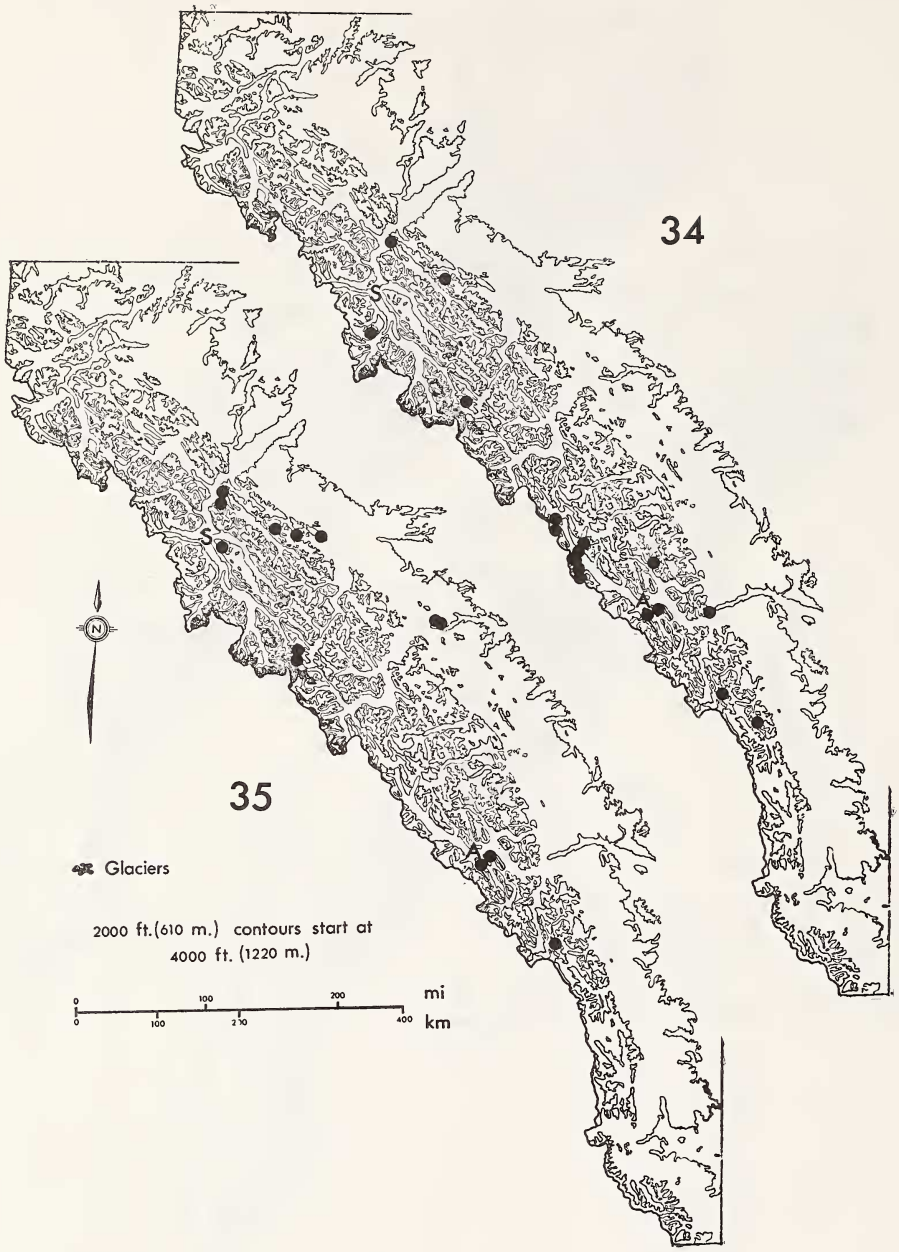
Figs. 28–29. Distribution of butterfly subspecies in Alberta.
A–Banff; S–Jasper. Fig. 28: *Boloria napaea reiffi*. Fig. 29: *Boloria improba youngi*.



Figs. 30–31. Distribution of butterfly species in Alberta.
A–Banff; S–Jasper. Fig. 30: *Boloria alberta*. Fig. 31: *Boloria astarte*.



Figs. 32–33. Distribution of butterfly subspecies in Alberta.
A–Banff; S–Jasper. Fig. 32: *Boloria eunomia nichollae*.Fig. 33: *Oeneis bore edwardsi*.



Figs. 34–35. Distribution of butterfly subspecies in Alberta.
A–Banff; S–Jasper. Fig. 34: *Oeneis melissa beani*. Fig. 35: *Onenis polixenes bruceï*.

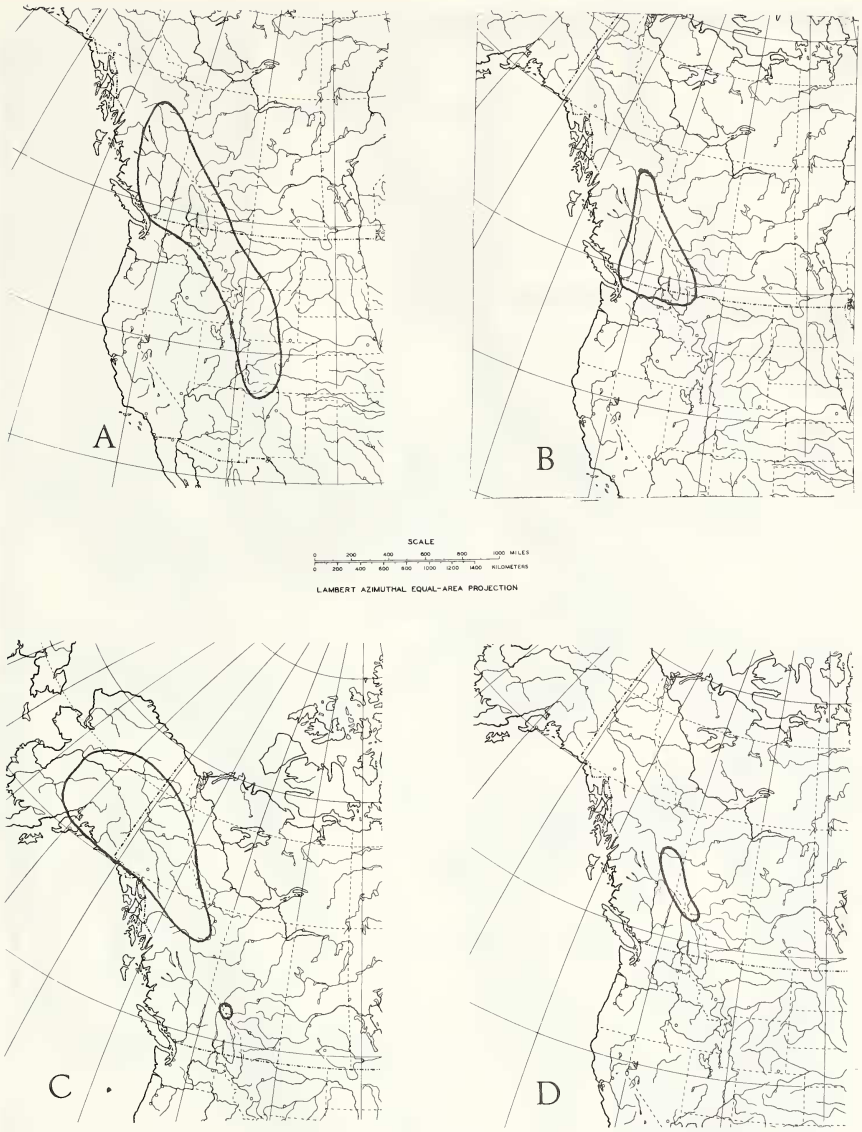


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Fig. 36: Distribution types exhibited by Alberta tundra butterflies.
A–Southern Montane; B–Central Montane; C–Disjunct populations; D–Endemic forms.

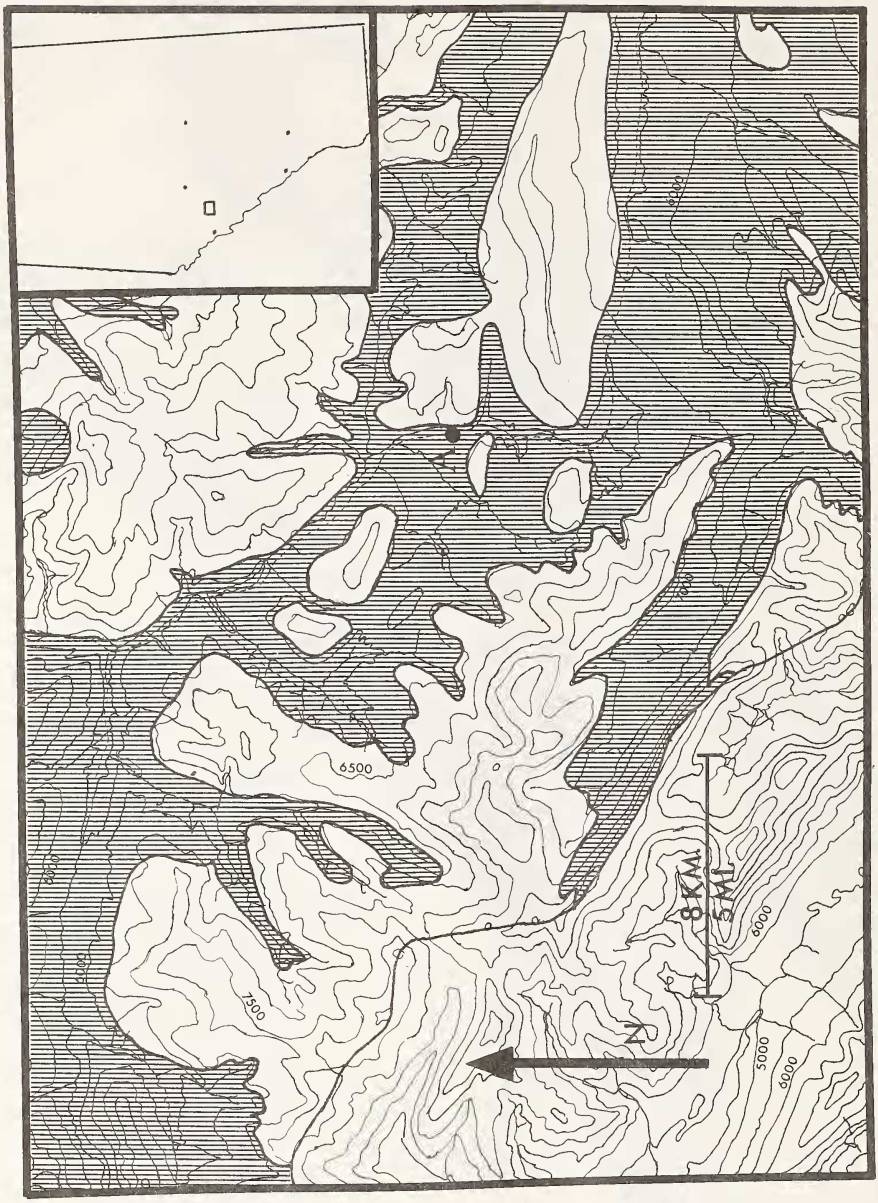

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Fig. 37: Extent of early Wisconsinan ice in the Mountain Park area. Hatching indicates presence of ice. Note extensive unglaciated areas above 6500 feet. Modified from data in Reimchen and Bayrock, 1977. The location of the town of Mountain Park is indicated by dot "A".

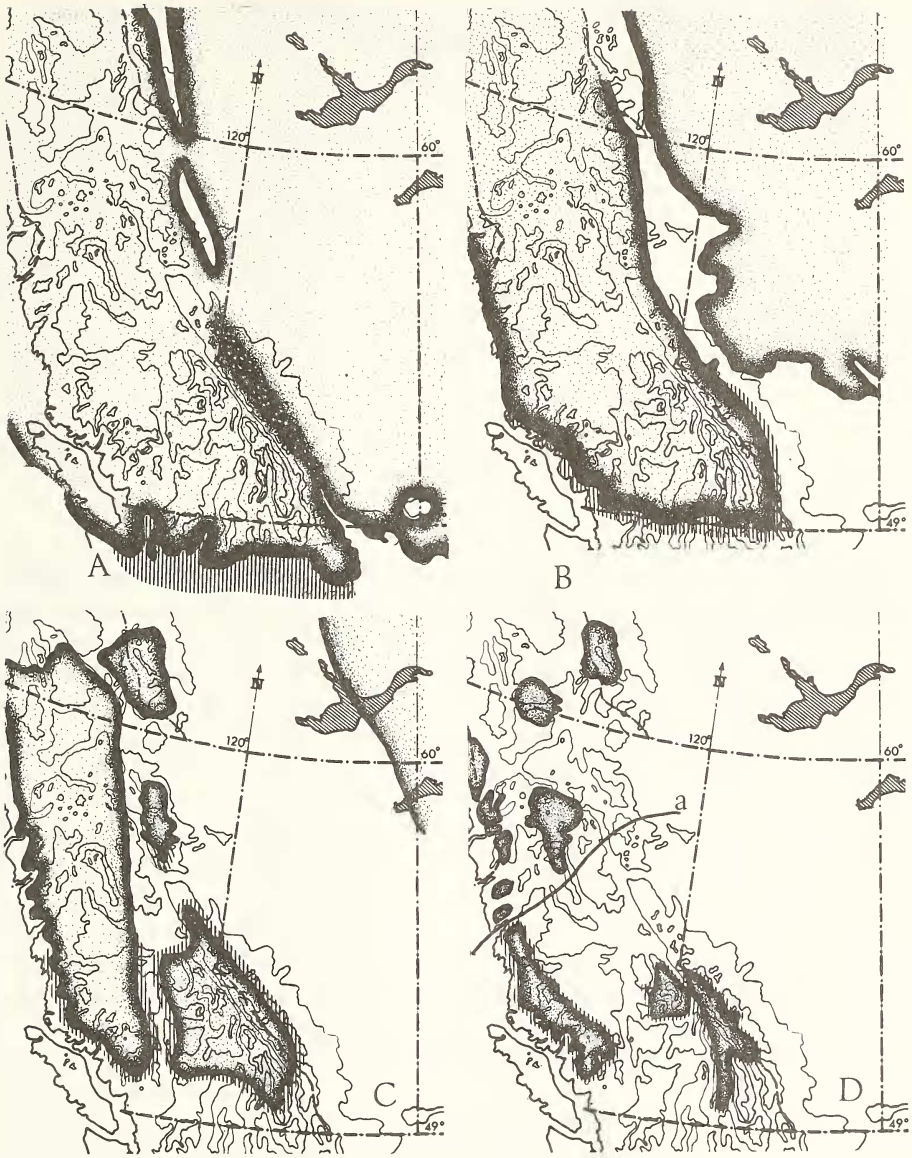

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Fig. 38: Retreat of Wisconsinan and recent ice sheets in Western Canada modified after Prest (1969).
A–17,000 to 15,000 years before present; B–12,000 years before present; C–10,000 years before present; D–8,000 years before present.
Stippled areas correspond to continental ice sheets. Colonization of Alberta by taxa in the refugium south of the ice sheets is indicated by vertical hatching. In C and D this tundra would be very narrow, perhaps less than 1 kilometer. In D, line 'a' indicates limit of northern dispersal.